THE PERFORMANCE OF FOUR NATIVE PERENNIAL FORB SPECIES ALONG A CLIMATE GRADIENT IN PACIFIC NORTHWEST PRAIRIES

by

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THESIS ABSTRACT

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Title: The Performance of Four Native Perennial Forb Species Along a Climate Gradient in Pacific Northwest Prairies

To determine how Pacific Northwest prairies are influenced by local site factors versus regional climate, we studied the reproduction, plant size, and density of sixteen natural populations of four perennial forb species native to Pacific Northwest prairies: *Ranunculus austro-oreganus, Sidalcea malviflora* spp. *virgata, Microseris laciniata,* and *Eriophyllum lanatum*. These populations were distributed along a 700 kilometer latitudinal gradient from southern Oregon to Whidbey Island, Washington. We found significant differences in plant size and reproduction among populations for all species, but correlations among edaphic and climate variables and plant size and reproduction were weak. Instead, density was more strongly correlated with both edaphic and climate variables, suggesting that this is a better indicator of long-term demographic processes. Although a few factors are important across species (e.g., nutrient availability and minimum temperature), response is idiosyncratic at the individual species level in Pacific Northwest prairies.

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CHAPTER I

INTRODUCTION

Climate Change and Species Distributions

Patterns in species distribution and community structure (i.e., which species are found where and in what combinations) are governed by multiple factors. One important factor is physiological tolerance limits to temperature and water availability (Kricher and Morrison 1988). For example, species that are adapted to survive in very dry environments may not do as well in wet environments, and vice versa (e.g., Larcher 1995, Grace 1997, Currie et al. 2004, Lambers et al. 2008, Kardol et al. 2010). Dispersal, the ability of seeds and other propagules to spread, is also an important factor in range distributions (Howe and Smallwood 1982, Howe and Westley 1997, Cain et al. 2000, Turnbull et al. 2000, Kubisch et al. 2014). This is particularly important for plants as sessile species; there may be areas that a given species would thrive in, but because it cannot reach those areas under natural dispersal processes, it is not naturally found there (Cunze et al. 2013). Habitat fragmentation further complicates dispersal for many species (e.g., Söndgerath and Schröder 2002, Pearson and Dawson 2005). Biotic interactions, ranging from predation to competition, also are a factor in determining the range of a species (HilleRisLambers et al. 2013, Wisz et al. 2013). Finally, stochastic events such as fire or severe storms, as well as anthropogenic disturbances, can strongly influence which species are found where (Crawley 1997, Schwilk and Keeley 2012, Ehrlén et al. 2016). As species distributions are governed by a number of complex factors and their interactions, it is difficult to predict where a species might be found under current

conditions. Predicting future distribution is even more difficult, given the increased uncertainty concerning future climate, in an increasingly fragmented landscape.

Nearly all of the factors that affect species ranges are directly or indirectly influenced by climate (Chen et al. 2011, Littell et al. 2011). Historically unprecedented changes in global temperature and precipitation patterns have been observed in the past century; the global average surface temperature (including both land and ocean areas) has increased by 0.85°C between 1880 to 2012 (IPCC 2013). In response to climate change, species from many taxa are shifting their geographic ranges (e.g., Parmesan 2006, Heller and Zavaleta 2009, Rapacciuolo et al. 2014). Species ranges can shift in two ways: they can expand beyond their current range limit, or they can contract from their current limit. Furthermore, different portions of the range limits (e.g., the northern range limit vs. the southern range limit) may respond differently. Different combinations of expansion and contraction at different ends of the range can result in overall expansion (expansion in one or more directions), overall contraction (contraction in one or more directions), or the range could maintain the same size and effectively shift (expansion in one direction and contraction in the other; Figure 1). If contraction is extreme, it eventually could result in extirpation or extinction of a species. All of these scenarios have been observed and attributed to climate change in recent decades (Doak and Morris 2010).

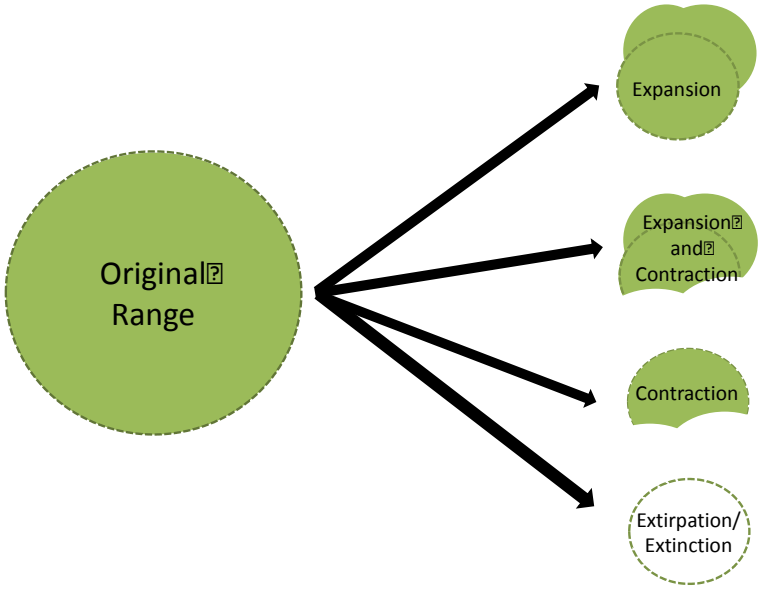


Figure 1. Possible range shifts. Different combinations of expansion and contraction result in four basic possible ways that ranges can change.

Meta-analyses of species showing biological responses to climate change found average range shifts from 6.1 kilometers per decade (Parmesan and Yohe 2003) to 17.6 kilometers per decade towards the poles (Chen et al. 2011). Similarly, the elevation at which species are found is reported to be increasing at average values ranging from 6.1 meters per decade (Parmesan and Yohe 2003) to 12.2 meters per decade (Chen et al. 2011). However, despite the overall trend, species responses are not always as expected, and taxonomy is not a good predictor of range shifts. For example, the ranges of some species are actually shifting opposite to predictions (VanDerWal et al. 2012, Rapacciuolo et al. 2014). Chen et al. (2011) attribute these differences in species' responses to three processes: (1) time delays in response; (2) variation in physiological constraints by species; and (3) other interacting drivers (e.g., habitat loss counteracting expansion due to warming). This work focuses primarily on the on the second of these processes: how physiological constraints may govern the response of individual species.

Global mean surface temperatures are expected to continue to rise in the next century; projected temperature increase ranges from 0.3ºC to 4.8ºC depending on the circulation model used (IPCC 2013). Furthermore, global precipitation patterns are expected to change, though the direction and magnitude of the change is expected to vary considerably with location (IPCC 2013). To predict how a particular species may respond to these anticipated changes in climate, it is necessary to understand the physiological, ecological, and environmental factors that are influencing current distributions. Using density, size, and reproduction as a proxy for fitness, we can infer which populations are located in the most favorable sites for a particular species, and which edaphic (soil-related) and/or climate characteristics contribute to making those sites suitable. This information ultimately facilitates prediction of which new areas will become suitable for a species and which portions of current ranges will become unsuitable, and thereby make informed management decisions based on expected expansion or contraction of the range of a species.

Mediterranean Climate and Prairies

Much of the western coast of the United States experiences a Mediterranean climate, with cool and wet winters and hot and dry summers (Cs, "warm temperate climate with dry summer"; Kottek et al. 2006). Regions with Mediterranean climate are hotspots of biodiversity; of the 25 hotspots identified by Myers et al. (2000), five are in Mediterranean climate zones. Together, these five regions support 20% of known plant diversity despite only covering 2% of Earth's land area (Klausmeyer and Shaw 2009). Although the global coverage of Mediterranean climate is projected to slightly increase, these regions are also among the most affected by land-use change, invasive species, and

habitat fragmentation, and the ability of plants native to these regions to adapt or colonize new areas is not known (Sala et al. 2000, Klausmeyer and Shaw 2009, Pfeifer-Meister et al. 2015).

One of the five biodiversity hotspots with a Mediterranean climate is found on the western coast of the United States. This hotspot, often referred to as the California Floristic Province, extends from California and into southern Oregon as the Klamath Mountains ecoregion. Within the Klamath Mountains ecoregion, the Rogue and Illinois valleys, in particular, are very similar to the Willamette Valley-Puget Trough-Georgia Basin ecoregion found to the north with warm to hot and dry summers alternating with cool and wet winters. Perennial bunchgrass-dominated prairie and oak savanna are important components of both the Klamath Mountains and Willamette Valley-Puget Trough-Georgia Basin ecoregions, and are the focus of this work (Floberg et al. 2004; ecoregions as defined by LandScopeAmerica and The Nature Conservancy). These communities are found along a narrow strip from British Columbia (Canada) to northern California (Floberg et al. 2004, Stanley et al. 2011, Pfeifer-Meister et al. 2015; Figure 2). This strip runs between the various coastal mountain ranges of the western coast of North America (i.e., the Oregon Coast Range and the Olympic Mountains) and the higher and farther inland Cascade Mountains. There is a natural climate gradient which parallels the latitudinal gradient in these two ecoregions; prairies found in the southern portions tend to be hotter and drier for longer than those found farther north (Reynolds et al. 2014, Pfeifer-Meister et al. 2015).

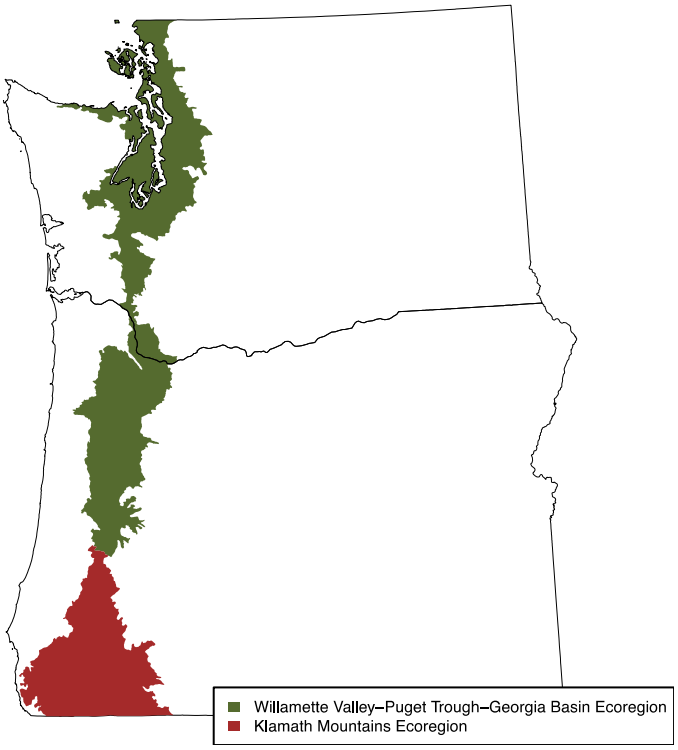


Figure 2. Location of the Willamette Valley-Puget Trough-Georgia Basin ecoregion and the Klamath Mountains ecoregion within Oregon and Washington.

In general, prairies are one of the most threatened ecosystems in the United States (Samson and Knopf 1994). Though very different from many of the prairies found elsewhere in the country (Pfeifer-Meister et al. 2008), the prairies of Washington and Oregon are similarly threatened (Noss et al. 1995). Thought to be a remnant of the warmer and drier climate of the early Holocene (approximately 11,000-7,250 years ago), these prairies were maintained by a combination of frequent wildland fire and burning by the Native American tribes that inhabited the region (Bachelet et al. 2011). Euro-American settlement starting circa 1850 reduced the frequency of fire, allowing tree species such as Douglas-fir (*Pseudotsuga menziesii*) to encroach on prairie (Agee 1993). Furthermore, Pacific Northwest prairies were often found on rich, fertile soils, which were quickly converted to agricultural uses by settlers, which further contributed to the

loss of prairie, as did invasion by non-native species (Christy and Alverson 2011). Today, less than 2% of the original area covered by prairie remains in the Willamette Valley, and prairie is similarly reduced throughout the ecoregion (Christy and Alverson 2011). Being able to predict how climate change will affect species within these communities is an important tool for conserving this threatened ecosystem.

CHAPTER II

CLIMATE CHANGE AND PACIFIC NORTHWEST PRAIRIES

Introduction

In the Pacific Northwest, an increase in annual mean temperature of 0.5–1.5°C has been observed over the past century (Bachelet et al. 2011). Temperature is projected to continue to increase 0.1°C to 0.6°C per decade with annual mean temperatures between 1.6°C and 3.0°C warmer by the 2080s (Mote and Salathé 2010). However, temperature change will not be evenly distributed throughout the year. Models predict that the greatest warming will occur in the summer (June–August) in the Pacific Northwest, though all months will warm (Mote and Salathé 2010).

Though changes in precipitation are not given as much attention in the discourse surrounding climate change (i.e., climate change is often referred to as global warming by the general public), a shift in the moisture regime could also have a significant impact on the geographic range of a species. Most models predict that precipitation in the Pacific Northwest will increase by up to 50% (Bachelet et al. 2011). However, the increase will not be evenly distributed throughout the year; most models predict that it will be concentrated in the fall, winter, and spring (September–May), which are already wet in the Pacific Northwest. In contrast, the already dry summer is expected to become drier (Mote and Salathé 2010). Combined with increased summer temperatures, decreased precipitation may lead to a reduction in soil moisture of up to 25% (Bachelet et al. 2011).

This research focuses on prairies in the interior valleys between the coastal mountain ranges on the east and the Cascade Range on the west. These native prairies are already at high risk of disappearance due to the alteration of historical fire regimes, land-

use change, and invasion by exotic species (Noss et al. 1995). Prior to Euro-American settlement in the mid-19th century, prairie covered approximately 49% of the Willamette Valley ecoregion in Oregon; today, it makes up less than 2% of the total land area, and the few remaining prairies are in degraded condition (Bachelet et al. 2011).

As a Mediterranean-type ecosystem, Pacific Northwest interior valley prairies are thought to be particularly vulnerable to climate change and may experience larger proportional losses of biodiversity than other terrestrial systems (Pfeifer-Meister et al. 2013, 2015). However, prairie species in the Pacific Northwest are already adapted to summer drought, and may not be significantly impacted by predicted increases in temperature and reductions in summer precipitation; thus they may be able to expand their range at the expense of adjacent forests which are less drought tolerant (Bachelet et al. 2011). Without careful examination of the system, it is difficult to predict the outcome under climate change, and a better understanding of how climate change will affect this important ecosystem is key to its conservation.

The question of how prairies in the Pacific Northwest will respond to predicted climate change is already under investigation. Pfeifer-Meister et al. (2013, 2015) experimentally manipulated both temperature and precipitation at three sites along a latitudinal gradient from southern Oregon to Washington (41-50°N) for three years, using 12 species with northern range limits in the study region to examine how demographic rates respond to experimental climate change. In general, the results of Pfeifer-Meister et al. (2013) suggest that prairie plants in the Pacific Northwest will not be as successful in their current range under projected climate change, and may need to shift their geographic distribution (Pfeifer-Meister et al. 2013). Although warming decreased

survivorship for all species, surviving plants produced more biomass under experimental warming; supplemental precipitation had very little effect on the demographic rates of the species observed (Pfeifer-Meister et al. 2013, 2015). The authors concluded that local factors, such as availability of nitrogen and phosphorous, were also important controls over biomass; availability of these resources was found to be controlled by both temperature and soil type (Wilson 2012, Pfeifer-Meister et al. 2013).

Manipulative experiments such as the one just described yield valuable information that can be applied to predicting range shifts, but also have limitations. For example, the lack of older individuals of perennial species in short-term studies is a major drawback (e.g., Pfeifer-Meister et al. 2013), as is the fact that some of the genotypes grown together in these experiments are highly unlikely to co-occur naturally (Nuismer and Gandon 2008, Moloney et al. 2009). Natural communities have also been observed to have very different reproduction patterns from experimental gardens (Harper 1977). Manipulative experiments are particularly limited by the scale and small number of treatments that are practical to study (e.g., Beier et al. 2012), and can unintentionally introduce other factors or have unintended effects on variables of interest (e.g., Carlyle et al. 2011, Elmendorf et al. 2015). Furthermore, communities established for short-term studies are often undergoing rapid succession that is not reflective of natural communities (e.g., Pfeifer-Meister et al. 2015). Observational studies using existing, naturally established populations are essentially substituting space for time; Fukami and Wardle (2005) note that there are fewer confounding factors with this experimental structure—particularly when geology and species are constant across the gradient—which can make it easier to determine if causal relationships are present. Finally, although it is beyond the

scope of this work, pairing natural populations and experimentally manipulated populations can lead to new insights into how plants will respond to climate change (Parmesan and Hanley 2015).

Here, we examined the biomass, reproduction, and plant density of natural populations of native prairie species along a natural 700 kilometer climate gradient in Pacific Northwest prairies. This work is part of a larger, multi-year study of the regional controls on prairie plant distributions under climate change in the Pacific Northwest, and is intended to supplement the work of Pfeifer-Meister et al. (2013, 2015). The primary focus of this research is to determine the relative strength of the factors determining the distribution of plants native to Pacific Northwest prairies. To do this, four species of perennial forbs were chosen for examination: *Ranunculus austro-oreganus* L.D. Benson (Southern Oregon buttercup), *Sidalcea malviflora* (DC.) A. Gray ex Benth. ssp. *virgata* (Howell) C.L. Hitchc. (rosy checkermallow), *Microseris laciniata* (Hook.) Sch. Bip. ssp. *laciniata* (cutleaf silverpuffs), and *Eriophyllum lanatum* (Pursh) Forbes (Oregon sunshine). These first three species were all included in Pfeifer-Meister et al.; *E. lanatum* was planted as part of the plant community used in that experiment, but was not studied. (2013, 2015). Multiple natural population of each species over a 700 kilometer latitudinal gradient were assessed to examine two main questions aimed at further elucidating how climate and local site factors affect prairie plants in the Pacific Northwest.

First, we asked whether edaphic (e.g., soil-related) or climatic variables are a stronger predictor of plant response in natural populations. In Pfeifer-Meister et al. (2013), heating resulted in more biomass and seed production, but the authors posited that this may have been due to an indirect effect of heating on nutrient availability. As

such, we expected that resource availability–a type of local variable–would be the primary determinant of size, density, and reproduction when comparing among natural populations, and climate would be of secondary importance. However, it is important to note that resource availability has been shown to be affected by local variables, such as soil type, as well as climate variables in Pacific Northwest prairies (Pfeifer-Meister and Bridgham 2007, Pfeifer-Meister et al. 2008, 2013). We expected this to be true for all four species included in this study.

Second, we asked to what extent climate affects density (plants per unit area), size (biomass), biomass density (biomass per unit area), and reproduction of prairie plant species in the Pacific Northwest. We expected that correlations among individual edaphic and climate variables and biomass would always be in the same direction as the correlations among those same variables and reproduction, as larger plants typically produce more flowers (Klinkhamer et al. 1992, Weiner et al. 2009, Qin et al. 2013). Similarly, because density is typically lower when plants are larger due to self-thinning (Stoll et al. 2002, Deng et al. 2012), we expected that correlations among site variables and biomass would be in the opposite direction of correlations among site variables and density. We hypothesized that that populations that experience higher temperatures would have larger plants (greater biomass), more biomass per unit area, and higher reproduction. Consequently, we expected that density would be lowest at the sites with the highest temperatures. Additionally, based on the finding of Pfeifer-Meister et al. (2013) that plants produced more biomass in plots with additional precipitation, we expected that populations that experience more precipitation in the winter and spring would have larger plants, higher reproduction, and more biomass per unit area.

By answering these questions, we can better understand which factors are the most important determinants of population size and structure, and make inferences about the most favorable conditions for plant species in Pacific Northwest prairies. When combined with results of other studies, this can ultimately allow predictions about the future of these species to be made.

Methods

Site Selection

We selected 16 populations at 12 sites (Figure 3; Table 1). The populations of each species selected for analysis are grouped into three regions, paralleling Pfeifer-Meister et al. (2013): southern Oregon (SOR), central Oregon (COR), and Washington (WAS). These regions are based on the northern range limits of the species selected–one species occurs no farther north than southern Oregon (*R. austro-oreganus*), another occurs in both southern and central Oregon (*S. malviflora* spp. *virgata*), the third occurs in both southern and central Oregon and has its northern range limit in Washington (*M. laciniata*), and the fourth is widespread (*E. lanatum*). These groups are referred to as Lowest Northern Limit (LNL), Intermediate Northern Limit (INL), Highest Northern Limit (HNL), and Widespread (W), respectively. We selected at least two populations in each region for each species where possible. However, for *M. laciniata* we were only able to locate one population that met our criteria in southern Oregon. Additionally, for the two species that only occur in one region (*R. austro-oreganus* and *S. malviflora* ssp. *virgata*), we located and censused three populations each.

All of the sites that we selected are native prairie remnants that have not been seeded to the best of our knowledge. Each site selected is as different as possible from

other sites for that species within the region to maximize the variation in abiotic factors (e.g., temperature, precipitation, aspect, etc.; Figure 4; Table 2). For example, in the case of *E. lanatum*, one central Oregon site is located in a wetland area at approximately 120 meters in elevation (Fisher Butte), and the other site is located in a bald with very shallow soil at approximately 750 m (Horse Rock Ridge).

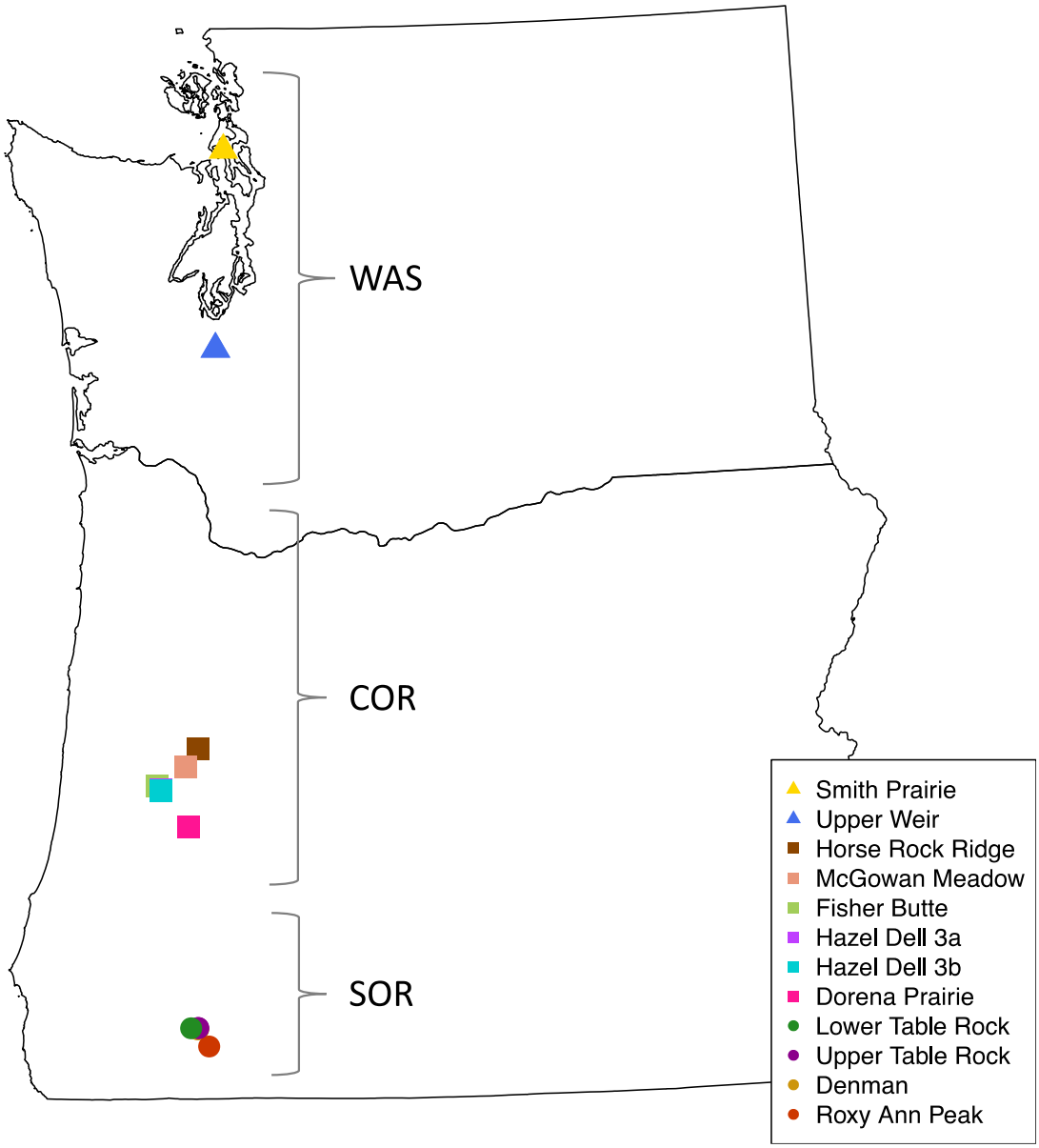


Figure 3. Approximate location of all populations included in study, with generalized regions shown.

Table 1. Species present at each site. Sites are in order of decreasing latitude.

Site	Site Region	*E. Lanatum (W)*	*M. laciniata (HNL)*	*S. malviflora* ssp. *virgata (INL)*	*R. austro-oreganus (LNL)*
Smith Prairie	WAS	X			
Upper Weir Prairie	WAS	X	X		
Horse Rock Ridge	COR	X			
McGowan Meadow	COR			X	
Fisher Butte	COR	X	X		
Hazel Dell 3a	COR			X	
Hazel Dell 3b	COR		X		
Dorena Prairie	COR			X	
Upper Table Rock	SOR	X			X
Lower Table Rock	SOR	X	X		
Denman Wildlife Area	SOR				X
Roxy Ann Peak	SOR				X
TOTAL NUMBER OF SITES		6	4	3	3

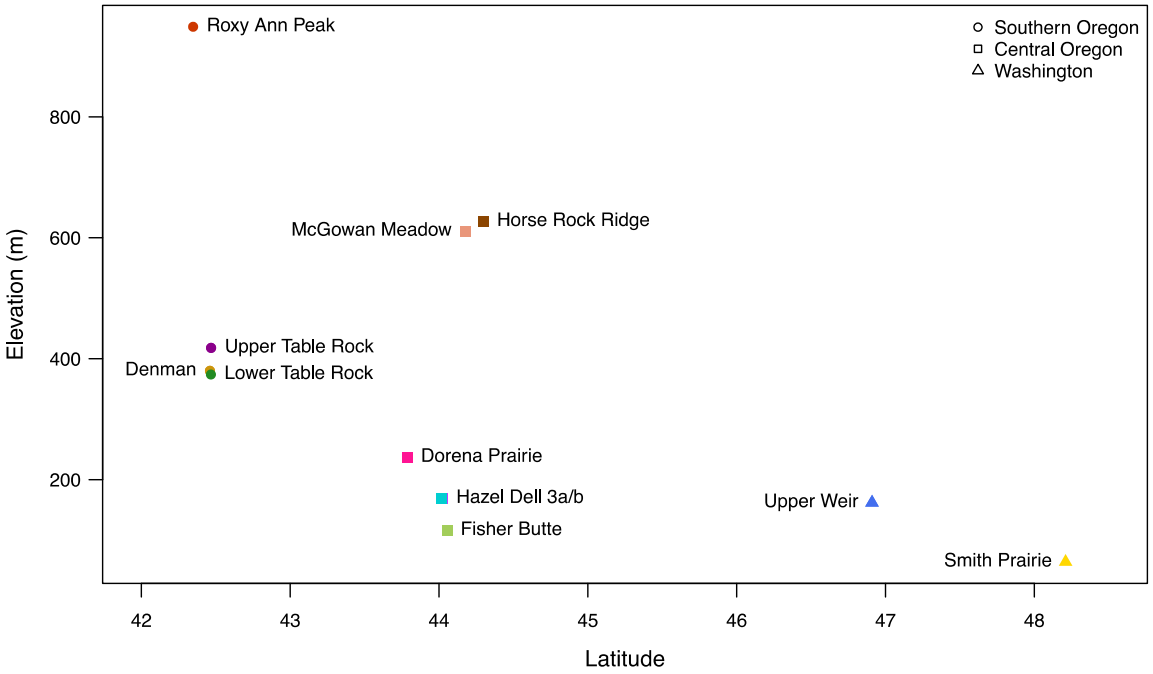


Figure 4. Elevation and latitude for all populations included in study.

Site Characterization

To characterize the physical environment at each site, a number of additional analyses were performed. We measured the depth of soil to obstruction at the beginning, middle, and end of each transect using a metal rod as a proxy for soil depth (referred to as "soil depth" for the remainder of this work). Soil pH, texture, bulk density, total carbon

and total nitrogen content were determined from soil samples taken from approximately 0-10 cm between March and May 2015. We collected two samples per transect for most sites, with the exception of Upper Table Rock and Upper Weir; at these two sites we collected a single sample for each transect. All soil samples were dried at 60°C for a minimum of 48 hours and sieved to 2 mm. However, only very large rocks were removed from the sample before measuring bulk density. We measured soil pH in a 1:1 by weight fresh soil to water slurry. For soil texture, we determined percent clay using the hydrometer method for a single sample for each transect (Gee and Bauder 1986). The sample was then sieved to 53 μm and weighed to determine percent sand; we calculated percent silt as the remainder when sand and clay were removed. We compared the measured textural class with the official taxonomic classification from the United States Department of Agriculture National Cooperative Soil Survey (USDA-NCSS) Soil Survey Geographic Database (SSURGO), which was accessed using the SoilWeb App (http://casoilresource.lawr.ucdavis.edu/gmap/). Total nitrogen and total soil carbon were measured with a Costech Analytical Technologies 4010 elemental combustion analyzer for each sample (Valencia, CA, USA); soil carbon to nitrogen ratio was calculated from this data.

Additionally, inorganic nitrogen (ammonium, NH_4^+ and nitrate, NO_3^-) was assessed using Plant Root Simulator (PRS) resin strips (Western Ag Innovations, http://www.westernag.ca), which measure anions and cations in situ. The PRS strips were incubated in situ for approximately four months from May to August; the actual burial period varied among the populations (range: 115-160 days).

Thirty-year averages (1981-2010) from the Parameter elevation Regression on Independent Slopes Model (PRISM) 800 meter resolution data set (PRISM Climate Group, Oregon State University) were used to determine long-term precipitation amounts and temperature averages for each site. We grouped monthly data into three seasons to better capture the seasonal differences in our Mediterranean system: November-February, March-June, and July-October. November-February encompasses fall green-up and the majority of winter rain; March-June captures spring green-up and the major growing season for most species. July-October encompasses the summer dry season.

Site Descriptions

Annual precipitation varies considerably among the twelve sites included in this study (Table 2). Although there is less variability among sites for annual maximum, mean, and minimum temperature, differences in seasonality clearly differentiate the sites (Table 2; individual species climate figures).

Ranunculus austro-oreganus Sites

R. austro-oreganus is endemic to southern Oregon, particularly the area around Medford (Benson 1954, Peck 1961, Seevers and Borgias 1993). As of 2016, it is a candidate for listing as a threatened or endangered species by the state of Oregon ("Oregon's threatened, endangered, and candidate plants" 2016). Consequently, all three *R. austro-oreganus* populations surveyed in this study are located within 10 miles of Medford (Figure 5). Roxy Ann Peak, located within the City of Medford's Prescott Park, rises nearly 700 meters above the valley floor; the *R. austro-oreganus* population located at this site is the highest population of any species included in this analysis (Figure 4).

Table 2. Annual precipitation, maximum temperature, mean temperature, and minimum temperature for all sites included in this study.

Site	Latitude	Location	Species Present	Annual Precipitation (mm)	Annual Maximum Temperature (˚C)	Annual Mean Temperature (˚C)	Annual Minimum Temperature (˚C)
Smith Prairie	48.21	WAS	*E. lanatum*	540.7	14.3	10.4	6.4
Upper Weir Prairie	46.909	WAS	*E. lanatum; M. laciniata*	1185.2	15.5	10.4	5.3
Horse Rock Ridge	44.298	COR	*E. lanatum*	2160	14.6	9	3.5
McGowan Meadow	44.177	COR	*S. malviflora* ssp. *virgata*	1931.5	15.3	9.8	4.3
Fisher Butte	44.054	COR	*E. lanatum; M. laciniata*	1133.1	17.3	11.4	5.5
Hazel Dell 3a	44.025	COR	*S. malviflora* ssp. *virgata*	1124.2	17.3	11.4	5.4
Hazel Dell 3b	44.02	COR	*M. laciniata*	1119.2	17.3	11.4	5.4
Dorena Prairie	43.787	COR	*S. malviflora* ssp. *virgata*	1175.7	17.3	11.2	5.2
Upper Table Rock	42.469	SOR	*E. lanatum; Ranunculus austro-oreganus*	575.2	19.9	12.3	4.7
Lower Table Rock	42.467	SOR	*M. laciniata*	557.5	20.2	12.6	5
Denman Wildlife Area	42.461	SOR	*E. lanatum; R. austro-oreganus*	564.2	20.1	12.6	5
Roxy Ann Peak	42.348	SOR	*R. austro-oreganus*	781.7	16.8	11	5.3

The populations at Upper Table Rock and Denman are considerably lower by over 500 meters. These two sites were located less than 1 kilometer apart, and are within adjacent grid cells in the PRISM dataset; therefore, they have nearly identical values for precipitation and minimum, mean, and maximum temperature (but different soil properties—see below). On an annual basis, Roxy Ann Peak has the smallest temperature range, with the warmest minimum temperature and the coolest maximum temperature. Upper Table Rock and Denman are generally warmer than Roxy Ann Peak by 2-3˚C in spring and summer, though the temperature difference is less pronounced during the winter (Figure 6). Maximum temperature can be as much as 4.4˚C cooler at Roxy Ann Peak (May), though the difference is never less than 1.3˚C (December; Supplemental Figure 1). However, in late summer and early winter minimum temperatures are higher at Roxy Ann Peak than at Denman and Upper Table Rock. Roxy Ann Peak receives over 200 mm more precipitation than either Upper Table Rock (Figure 6; Table 2); the difference in concentrated in winter in spring, when Roxy Ann Peak receives more rain in winter and spring than the other two sites by 15-30 mm each month. All three sites receive similarly minimal precipitation in July (approximately 13 mm).

All three *R. austro-oreganus* populations are located in open prairie and oak savanna on slight slopes. All three of these sites are on Mollisols or Vertisols (Table 3). Both Roxy Ann Peak and Denman have greater than 43% clay. Soils are over twice as deep at Roxy Ann Peak than at either other site. Both total nitrogen and total carbon are highest at Upper Table Rock and lowest at Roxy Ann Peak, though Roxy Ann Peak and Denman are not substantially different. Plant available nitrogen is dominated by nitrate at

all three sites, and is over three times higher at Denman than at Upper Table Rock, the next highest site (Figure 8).

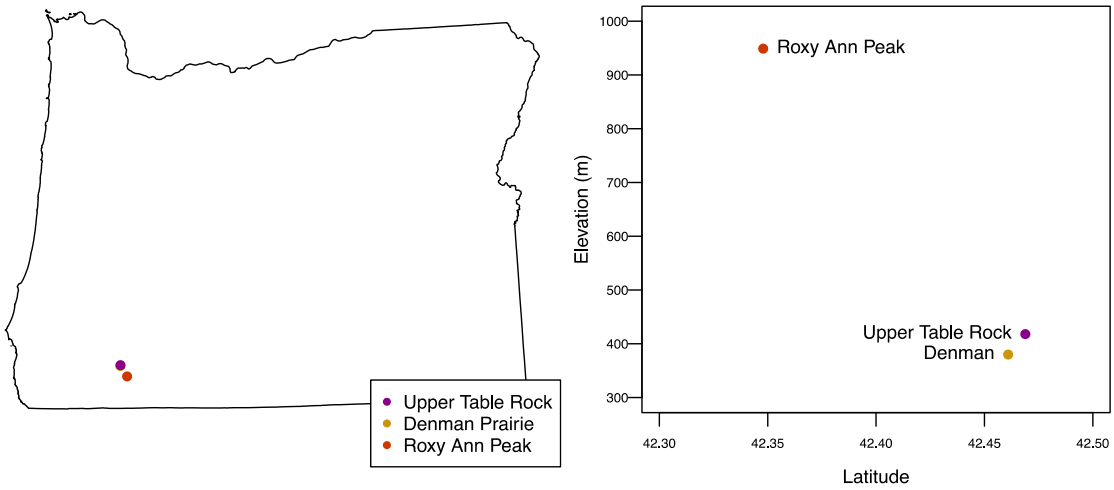


Figure 5. Location and elevation of the *R. austro-oreganus* populations. Note that Upper Table Rock and Denman Prairie are located so close together they appear to be one site at this scale.

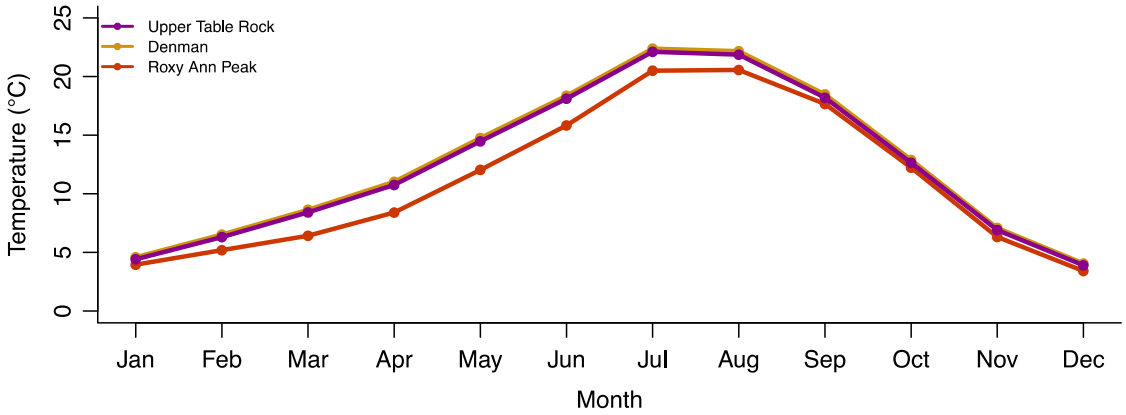


Figure 6. Monthly mean temperature for the three sites with *R. austro-oreganus* populations based on 30-year normals (1980-2010). Note that Upper Table Rock and Denman Prairie are located so close together that they have nearly identical temperatures throughout the year.

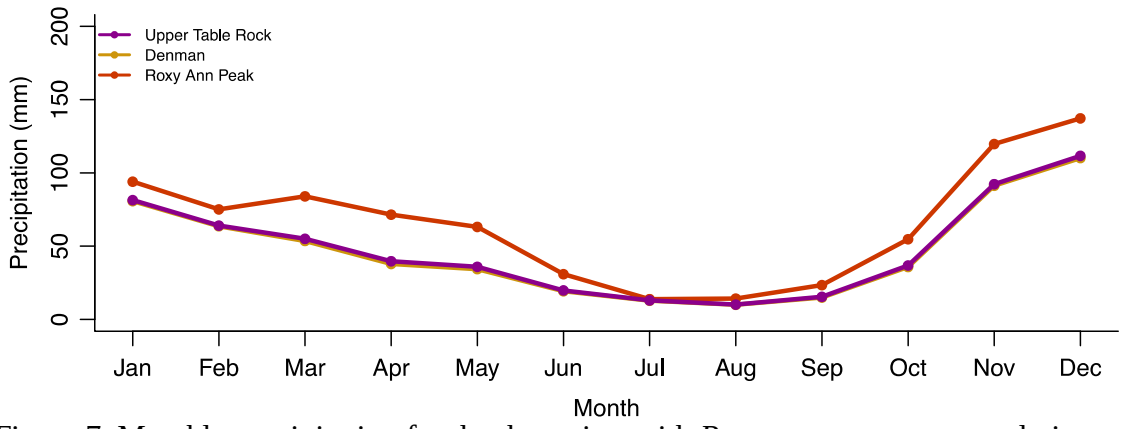


Figure 7. Monthly precipitation for the three sites with *R. austro-oreganus* populations based on 30-year normals (1980-2010). Note that Upper Table Rock and Denman Prairie are located so close together that they receive nearly the same amount of precipitation the year.

Table 3. Soil description and characteristics for the three sites with *R. austro-oreganus* populations. Where appropriate, numbers in parentheses indicate one standard error.

Site	Roxy Ann Peak	Denman	Upper Table Rock
Taxonomy	Fine, smectitic, mesic Vertic Haploxerolls	Fine, smectitic, mesic Typic Chromoxererts	Fine, smectitic, mesic Typic Chromoxererts; Clayey-skeletal, smectitic, mesic Pachic Argixerolls
Series	Heppsie Clay	Carney Clay	Carney-Table Rock Complex Loam
Texture - Sand (%)	7.5	18.0	33.7
Texture - Clay (%)	56.0	43.4	19.2
Texture - Silt (%)	36.5	38.5	47.1
pH	7.2	7.1	7.0
Soil Depth (cm)	>80	29.2	17.0
Bulk Density (g/cm^3)	1.07	1.20	1.05
Total Nitrogen (%)	0.09 (0.02)	0.11 (0.03)	0.16 (0.05)
Total Carbon (%)	1.19 (0.22)	1.24 (0.32)	2.20 (0.63)

Sidalcea malviflora ssp. virgata Sites

The three *S. malviflora* ssp. *virgata* populations are all located in central Oregon, within 30 miles of the city of Eugene (Figure 9). This reflects the range of the species in central Oregon; although it historically could be found in northern Umpqua Valleys, we were unable to locate any populations outside of Lane County (Peck 1961). Although

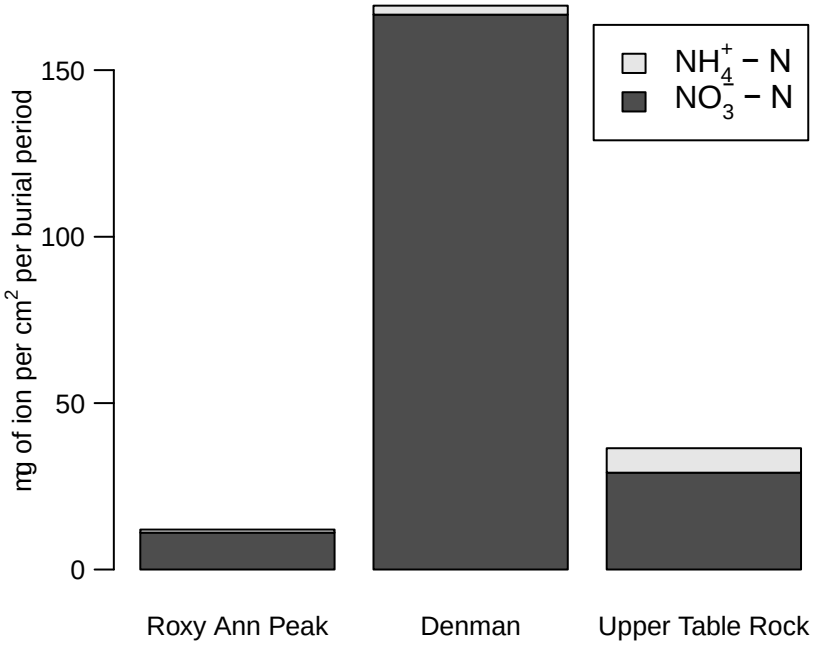


Figure 8. Plant available nitrogen, May-August, for the three sites with *R. austro-oreganus* populations.

Dorena Prairie and Hazel Dell 3a are approximately 50 kilometers apart and Dorena Prairie is 68 meters higher than Hazel Dell 3a, these two sites have nearly identical mean temperatures throughout the year (Figure 10). They also exhibit similar precipitation patterns, though Dorena Prairie is slightly wetter in the spring and summer and drier in the winter and overall receives approximately 50 mm more precipitation on an annual basis. In contrast, McGowan Meadow is located at high elevation (611 meters) within the Coburg Hills. Not surprisingly, given its higher elevation and more northern location, thissite has the lowest mean temperatures and highest precipitation throughout the year. Mean temperatures are consistently 1-2˚C cooler than Dorena Prairie and Hazel Dell 3a; the difference can be even greater for maximum temperatures, particularly in late winter and early spring (Supplemental Figure 2). Minimum temperatures follow a similar pattern, though the minimum temperature is nearly identical at all three sites in September and October. The Mediterranean climate regime is much more pronounced at

McGowan Meadow; it receives much higher rainfall in the winter and spring, but similar amounts of precipitation in the summer when compared to the two other sites (Figure 11).

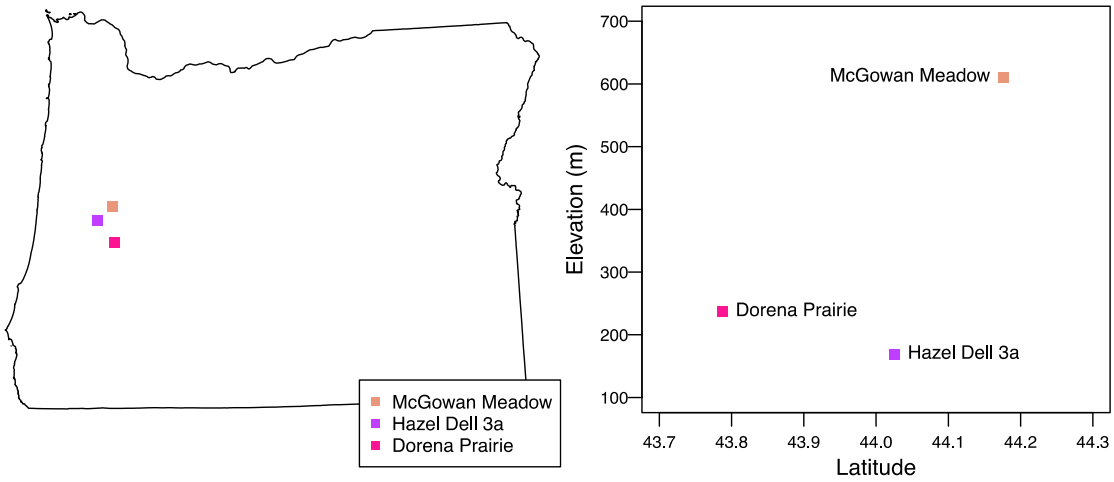


Figure 9. Location and elevation of the *S. malviflora* ssp. *virgata* populations.

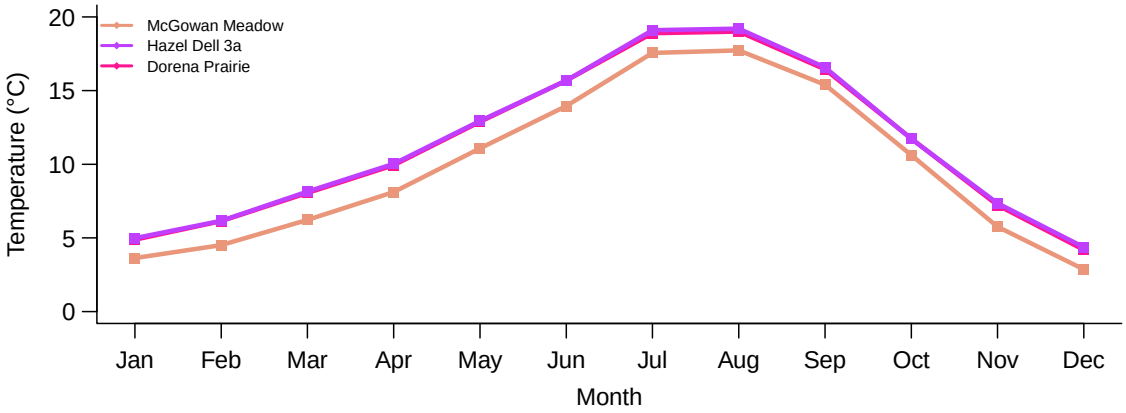


Figure 10. Monthly mean temperature for sites with *S. malviflora* ssp. *virgata* populations based on 30-year normals (1980-2010). Note that Hazel Dell 3a and Dorena Prairie have nearly identical temperatures throughout the year despite their geographic separation.

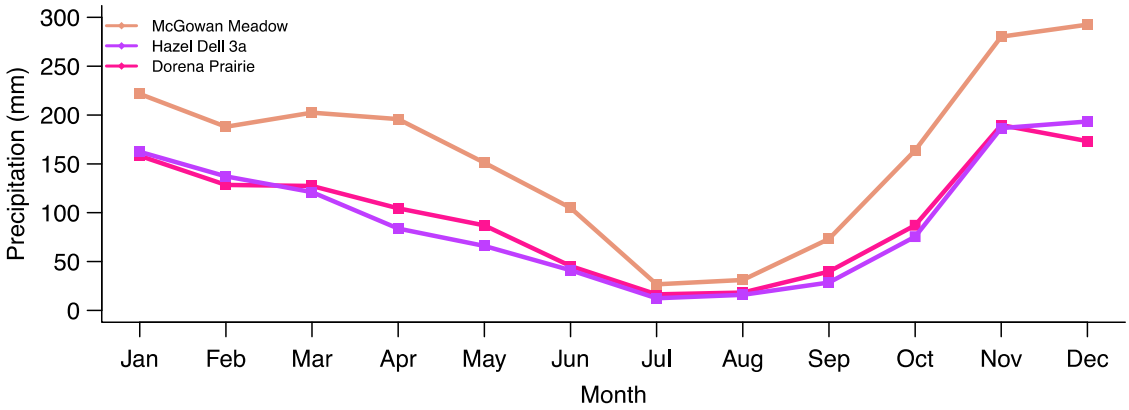


Figure 11. Monthly precipitation for sites with *S. malviflora* ssp. *virgata* populations based on 30-year normals (1980-2010).

While both Hazel Dell 3a and Dorena Prairie are located on Mollisols, the soils typical of prairies, McGowan Meadow is located on an Ultisol (Table 5). Additionally, the soil is deepest (greater than 80 cm) and the bulk density is also highest at McGowan Meadow. Though soils at Dorena Prairie and Hazel Dell 3a have similar bulk densities, soil depth is much less at Dorena Prairie. Total nitrogen and total carbon are greatest at McGowan Meadow and lowest at Hazel Dell 3a. However, the amount of inorganic nitrogen available to plants is highest at Hazel Dell 3a, and is over twice as high as at McGowan Meadow, the site with the least inorganic nitrogen (Figure 12). At Dorena Prairie, ammonium dominates; nitrate is the dominant source of plant available nitrogen at Hazel Dell 3a and McGowan.

Microseris laciniata Sites

M. laciniata is found from California to Washington's Puget Sound, typically on moist ground (Peck 1961); the four sites in this study are distributed throughout this range. The southernmost site, Lower Table Rock, is also the highest (Figure 13). It experiences the highest maximum and mean temperatures of the four *M. laciniata* populations; the difference between it and the other sites is greatest in the summer and

Table 4. Soil description and characteristics for the three sites with *S. malviflora* ssp. *virgata* populations. Where appropriate, numbers in parentheses indicate standard error.

Site	Dorena Prairie	Hazel Dell 3a	McGowan Meadow
Taxonomy	Fine-silty, mixed, mesic Cumulic Ultic Haploxerolls	Fine, mixed, mesic Pachic Ultic Argixerolls; Clayey, smectitic, mesic, shallow Vertic Haploxerolls; very-fine, mixed, mesic Aquultic Haploxerolls	Fine, mixed, mesic Typic Umbraqualfs OR Cumley; Clayey, mixed, mesic Typic Haplohumults
Series	Chehalis Sandy Clay Loam	Dixonville-Philomath-Hazelair Complex Loam	Minniece Silt Loam
Texture - Sand (%)	54.8	39.0	32.8
Texture - Clay (%)	21.8	22.4	11.8
Texture - Silt (%)	23.5	38.6	55.4
pH	6.9	6.5	6.3
Soil Depth (cm)	25.8	73.1	>80
Bulk Density (g/cm^3)	0.99	0.95	1.29
Total Nitrogen (%)	0.347 (0.01)	0.292 (0.01)	0.389 (0.02)
Total Carbon (%)	4.852 (0.36)	3.612 (0.09)	5.878 (0.32)

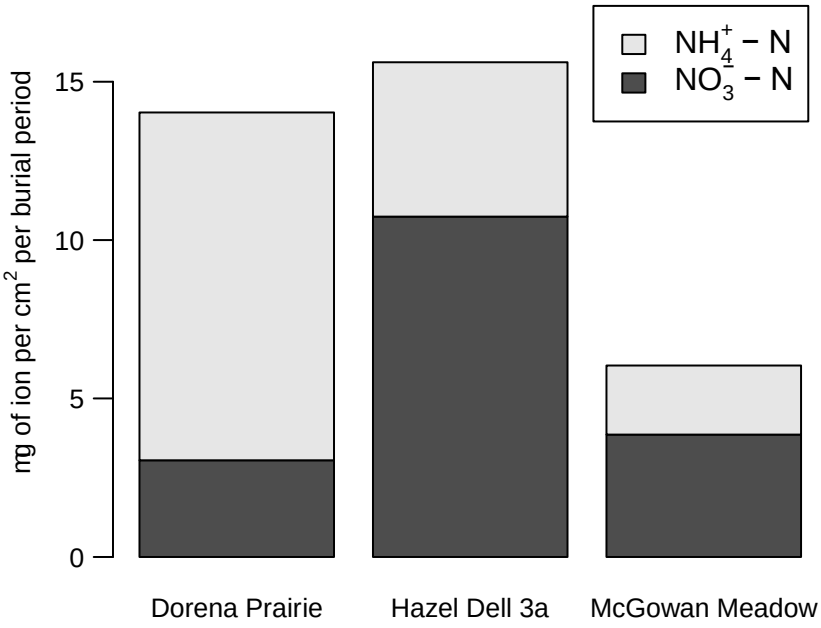


Figure 12. Plant available nitrogen, May-August, for sites with *S. malviflora* ssp. *virgata* populations.

least in winter; it can be as much as 8˚C warmer than the northernmost site, Upper Weir (Table 2; Figure 14). However, minimum temperatures for Lower Table Rock are the coldest of all four sites from October through February, and this site has the coldest annual minimum temperature (Table 3; Supplemental Figure 3). The two central sites,

Fisher Butte and Hazel Dell 3b, are within 5 kilometers of each other and only differ in elevation by approximately 50 meters; climate data for these two sites is nearly identical. The difference in mean temperatures is consistently 0.5-1.5˚C for Fisher Butte/Hazel Dell 3b and Upper Weir. Annual precipitation is not substantially different between the central Oregon and Washington sites, and the same general seasonal pattern holds for these three sites, with the most precipitation in November and December and the least in July and August (Table 2; Figure 15). In contrast, annual precipitation at Lower Table Rock is much lower, and while the same seasonal pattern holds, there is much less variation in the amount of precipitation received each month. All four sites receive similar amounts of rain in July and August, the driest months. It is interesting to note that Fisher Butte is a seasonal wetland and often has standing water in the winter.

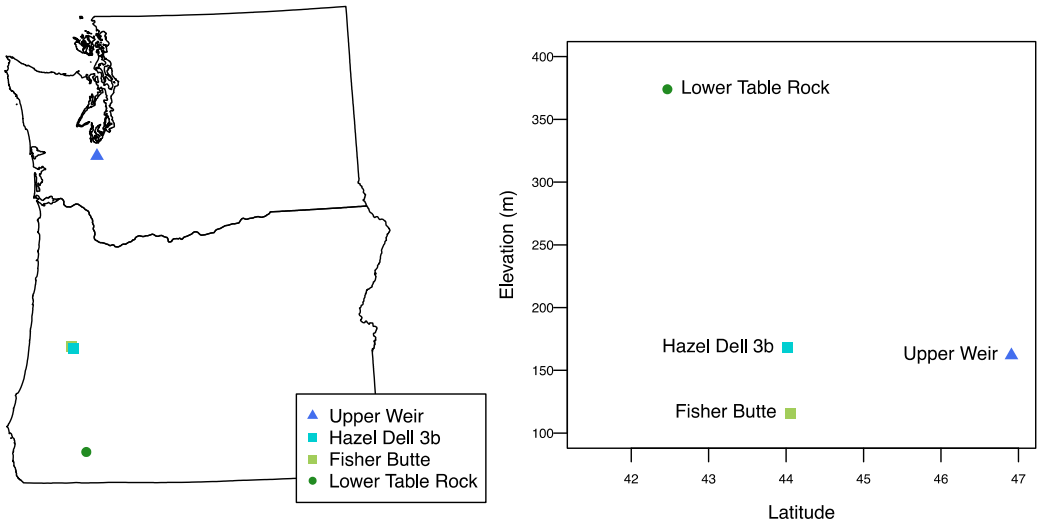


Figure 13. Location and elevation of the *M. laciniata* populations.

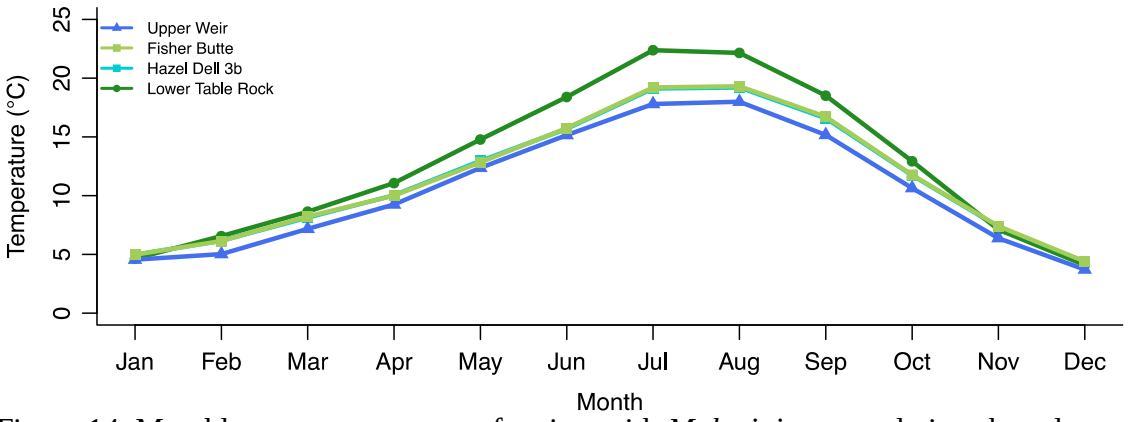


Figure 14. Monthly mean temperature for sites with *M. laciniata* populations based on 30-year normals (1980-2010). Note that Hazel Dell 3b and Fisher Butte have nearly identical temperatures throughout the year despite their geographic separation.

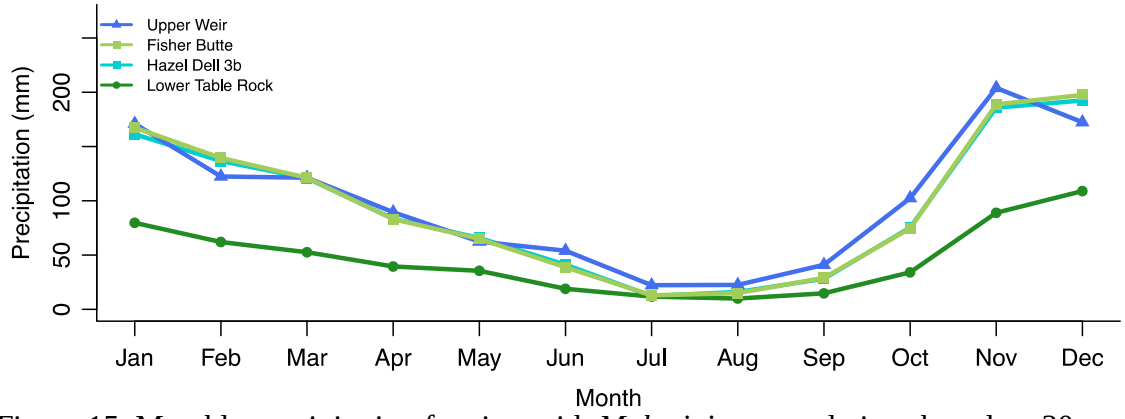


Figure 15. Monthly precipitation for sites with *M. laciniata* populations based on 30-year normals (1980-2010). Note that Hazel Dell 3b and Fisher Butte receive nearly identical amounts of precipitation throughout the year despite their geographic separation.

All three Oregon sites are located on high-chroma Vertisols, which often indicates a low organic matter content in the soil (Brady and Weil 2004). In contrast, Upper Weir is located on an Inceptisol with a high organic matter content (Table 6). Similarly, total carbon content is much higher at Upper Weir than at any of the Oregon sites; total nitrogen follows a similar pattern. Inorganic nitrogen is highest at Upper Weir and lowest at Fisher Butte (Figure 16). Although Lower Table Rock has the lowest amount of total nitrogen, it has the second highest plant-available nitrogen. At all four sites the inorganic nitrogen is dominated by nitrate, though the amounts of ammonium and nitrate are nearly

equal at Upper Weir. Upper Weir also has a much higher sand content and lower bulk density than the other sites. Soil depth varies substantially across all four sites; it is deepest at Fisher Butte and shallowest at Lower Table Rock.

Table 5. Soil description and characteristics for the four sites with *M. laciniata* populations. Where appropriate, numbers in parentheses indicate standard error.

Site	Lower Table Rock	Hazel Dell 3b	Fisher Butte	Upper Weir
Taxonomy	Fine, smectitic, mesic Typic Chromoxererts	Very-fine, smectitic, mesic Aquic Chromoxererts	Very-fine, smectitic, mesic Aquic Chromoxererts	Sandy-skeletal, isotic, mesic Typic Humixerepts
Series	Carney Silt Loam	Natroy Loam	Natroy Silt Loam	Spanaway Loamy Fine Sand
Texture - Sand (%)	43.0	32.7	26.5	81.3
Texture - Clay (%)	20.5	19.9	11.6	0.0
Texture - Silt (%)	36.4	47.4	61.9	18.7
pH	6.8	6.3	5.4	5.5
Soil Depth (cm)	10.8	72.8	>80	27.5
Bulk Density (g/cm^3)	1.14	0.81	1.09	0.50
Total Nitrogen (%)	0.15 (0.01)	0.33 (0.03)	0.22 (0.01)	0.93 (0.05)
Total Carbon (%)	2.46 (0.31)	4.13 (0.37)	2.47 (0.19)	13.16 (0.62)

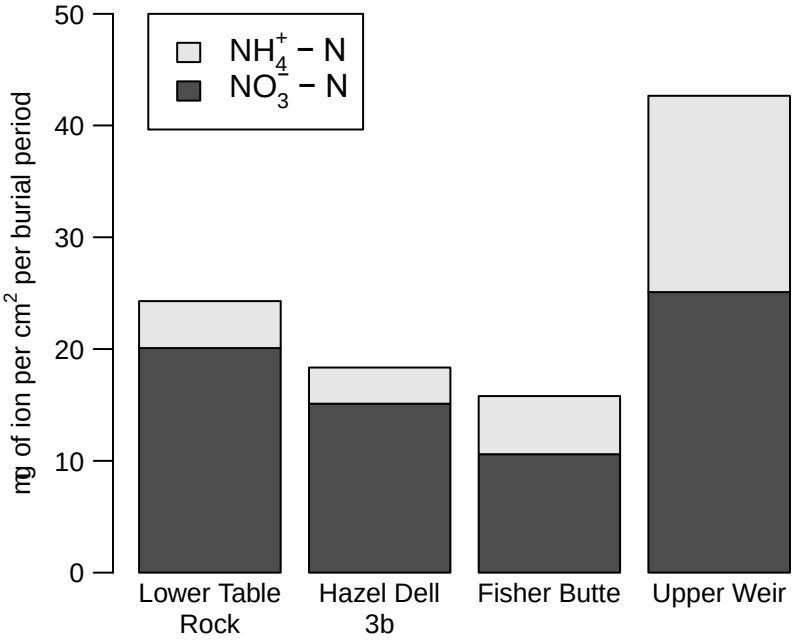


Figure 16. Plant available nitrogen, May-August, for sites with *M. laciniata* populations.

Eriophyllum lanatum Sites

E. lanatum is found throughout the western half of the United States and Canada (Peck 1961, James C. Hickman 1993); the six populations included in this study are across a 600 kilometer gradient from southern Oregon to northern Washington (Figure 17). The highest population, Horse Rock Ridge, is located in central Oregon's Coburg Hills at 627 meters; the lowest population at 64 meters, Smith Prairie, is also the northernmost. Additionally, Smith Prairie is located on Whidbey Island in Washington's Puget Sound, within the rain shadow of the Olympic Peninsula. Temperatures on Whidbey Island are moderated by its proximity of the waters of Puget Sound; this site has the least variation in temperature throughout the year, as well as the smallest differences among minimum, mean, and maximum temperatures (Table 2; Figure 18; Supplemental Figure 4).

Annual temperatures vary considerably among the six sites with *E. lanatum* populations (Table 2). The spread among the annual maximum temperatures at the six populations (~6˚C) is much greater than the spread among annual minimum temperatures at the six populations (~2.5˚C). Seasonal temperature patterns broadly follow the same general trend of warmer summers and cooler winters at all sites, but the magnitude of seasonal changes varies by site and the differences among sites vary throughout the year; the warmest sites in the summer are often among the cooler sites in the winter (Figure 18). Horse Rock Ridge experiences the lowest temperatures of all sites included in this analysis; during the coldest month, December, temperatures can be less than -1˚C. Horse Rock Ridge also experiences the greatest variation in precipitation, with over twice as much precipitation as the southern Oregon sites and Smith Prairie in winter, but similar

amounts of precipitation in the summer (Figure 19). Fisher Butte and Upper Weir experience similar amounts of precipitation despite being located over 300 kilometers apart; this amount is intermediate between that of Horse Rock Ridge and the other sites.

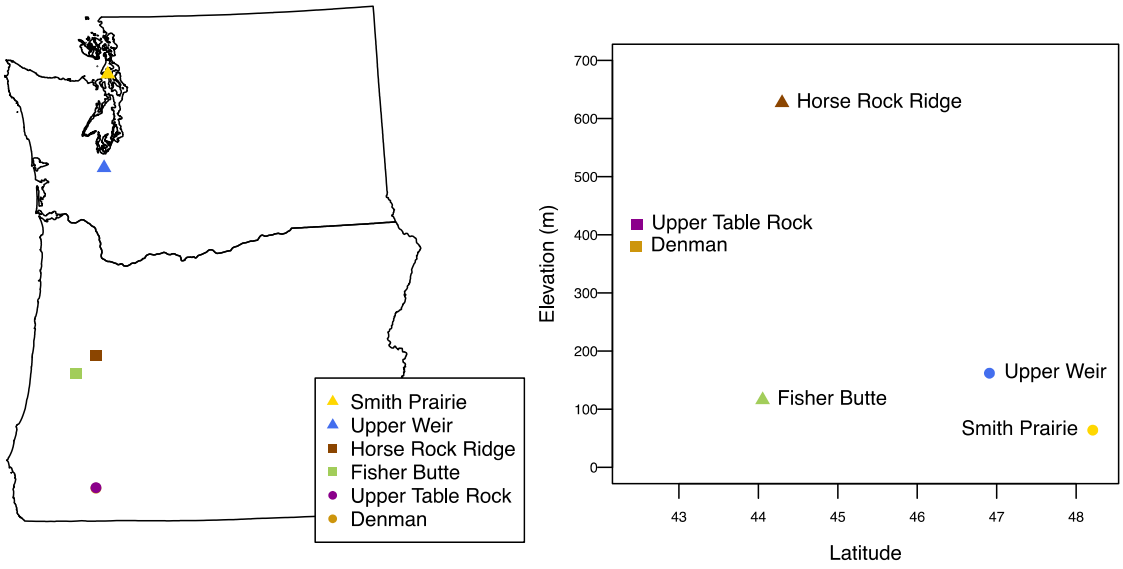


Figure 17. Location and elevation of the *E. lanatum* populations.

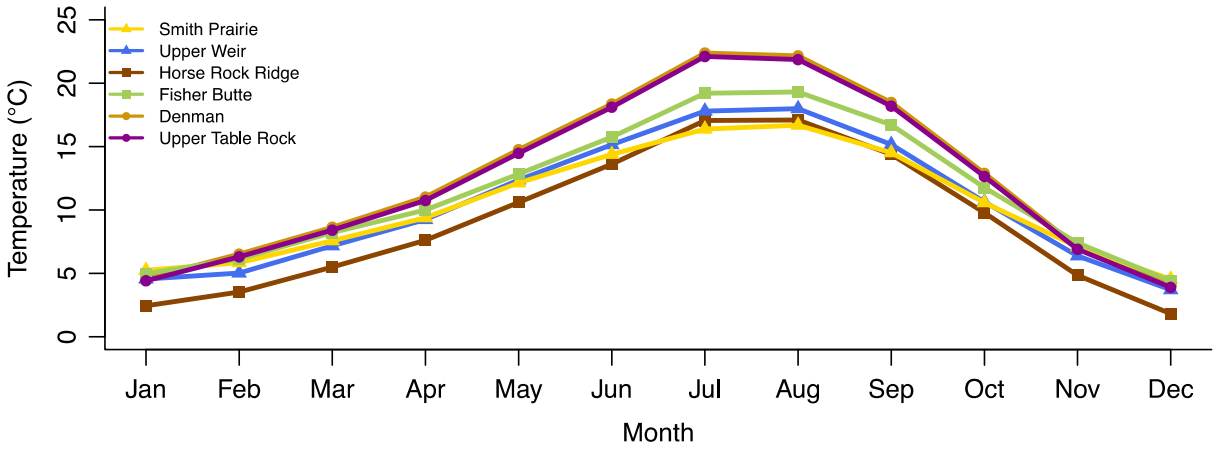


Figure 18. Monthly mean temperature for sites with *E. lanatum* populations based on 30-year normals (1980-2010). Note that Upper Table Rock and Denman Prairie are located so close together that they have nearly identical temperatures throughout the year.

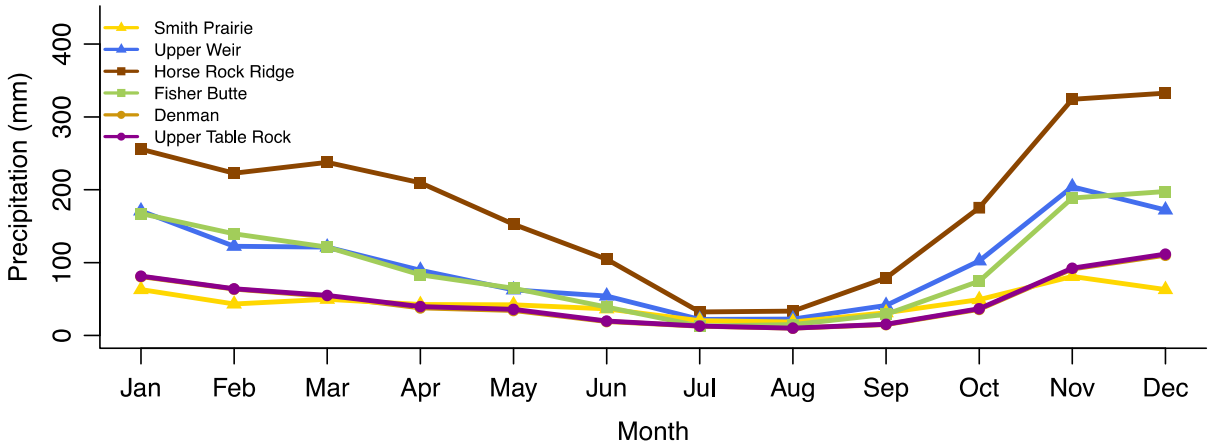


Figure 19. Monthly precipitation for sites with *E. lanatum* populations based on 30-year normals (1980-2010). Note that Upper Table Rock and Denman Prairie are located so close together that they receive the same amount of precipitation throughout the year.

Soil type and characteristics vary considerably from site to site. Vertisols and Mollisols are the most common soil orders, though Upper Weir is located on an Inceptisol and Horse Rock Ridge is located on an Entisol (Table 6). Upper Weir and Horse Rock Ridge also have much lower bulk densities than the other sites. The Washington sites, as well as Horse Rock Ridge, have a high content of sand (over 75%). Denman has the highest clay content of any of these sites by a large margin, and the most plant available nitrogen of any site by a substantial margin. However, total nitrogen is lowest at Denman and highest at Upper Weir and Horse Rock Ridge (Figure 20). At all sites, inorganic nitrogen is primarily composed of nitrate. Horse Rock Ridge, Smith Prairie, and Upper Weir also have much higher total carbon than the other three sites.

Table 6. Soil description and characteristics for the six sites with *E. lanatum* populations. Where appropriate, numbers in parentheses indicate standard error.

Site	Denman	Upper Table Rock	Fisher Butte	Horse Rock Ridge	Upper Weir	Smith Prairie
Taxonomy	Fine, smectitic, mesic Typic Chromoxererts	Fine, smectitic, mesic Typic Chromoxererts; Clayey-skeletal, smectitic, mesic Pachic Argixerolls	Very-fine, smectitic, mesic Aquic Chromoxererts	Mesic Orthoents (Rock Outcrop)	Sandy-skeletal, isotic, mesic Typic Humixerepts	Sandy, isotic, mesic Pachic Ultic Haploxerolls
Series	Carney Clay	Carney-Table Rock Complex Loam	Natroy Silt Loam	Loamy Fine Sand	Spanaway Loamy Fine Sand	San Juan Fine Sand
Texture - Sand (%)	18.0	33.7	26.5	75.3	81.3	86.7
Texture - Clay (%)	43.4	19.2	11.6	1.3	0.0	2.5
Texture - Silt (%)	38.5	47.1	61.9	23.4	18.7	10.8
pH	7.1	7.0	5.4	6.0	5.5	6.0
Soil Depth (cm)	29.2	17.0	>80	34.5	27.5	37.1
Bulk Density (g/cm^3)	1.20	1.05	1.09	0.47	0.50	0.92
Total Nitrogen (%)	0.11 (0.01)	0.15 (0.01)	0.22 (0.01)	0.79 (0.01)	0.93 (0.05)	0.54 (0.04)
Total Carbon (%)	1.32 (0.11)	1.95 (0.09)	2.47 (0.19)	9.74 (0.80)	13.16 (0.62)	7.41 (0.69)

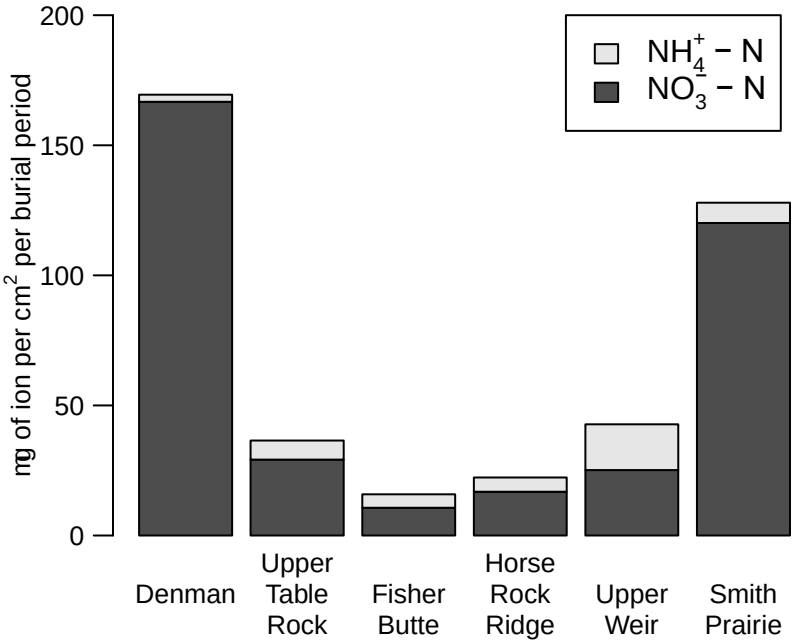


Figure 20. Plant available nitrogen, May-August, for sites with *E. lanatum* populations.

Allometric Equation Development

To approximate biomass without killing plants, we developed allometric equations relating non-destructive field measurements with actual biomass. To develop these equations, we measured and harvested approximately 30 plants per species for *E. lanatum*, *M. laciniata*, and *S. malviflora* ssp. *virgata*. For each species, all plants were harvested from a single site. However, due to constraints on destructive sampling, we were not able to harvest and weigh plants in the entire range of sizes observed. In particular, very large plants, especially of *E. lanatum*, were undersampled.

Plants were oven dried at 60°C for a minimum of 48 hours prior to weighing. We then performed stepwise regression with R's (Version 3.2.2, R Core Team 2015) *step()* function on the training data set, using exhaustive, forward, and backward selection and the Akaike Information Criterion. We applied the resulting equation to each population of the species in question to verify that it yielded reasonable biomass values. In a few cases, the original equation developed yielded nonsensical results (e.g., negative biomass); in

those cases, we were able to return to the stepwise selection process and modify the equation with very little reduction in explanatory power.

A similar procedure was used to develop an allometric equation for *R. austro-oreganus* in 2010; 473 plants, harvested from the experimental plots, were used to develop that equation (Fegan 2010, unpublished).

Demographic Censuses

We censused each population once between March and June 2015, as close as possible to when the plants were approaching the end of their maximum flowering period and had begun to set seed (Supplemental Table 1). At each population, we marked approximately 200 individual plants with painted nails along transects ranging from 1-30 m long (depending on density), and then collected data related to biomass and reproduction (e.g., size of largest leaf, number of leaves, number of flowering stems, number of flowers, seeds per flower, etc.). We also recorded presence/absence of several damage types for each plant (e.g., grazing and pathogens) to allow for an assessment of biotic controls; the total number of types of damage was then calculated. For the majority of each transect, we marked and measured every plant within a set distance of the transect, allowing for analysis of density and related characteristics. For portions of some transects we marked and measured additional plants to have every age-class evenly represented in the dataset for later demographic analysis; these plants are not included in the analyses described here.

Additionally, the three *R. austro-oreganus* populations were also visited a second time to capture information on fruiting because they were initially measured too early (Supplemental Table 1). For Roxy Ann Peak, we updated reproduction data (number of

flowers/buds and fruits) for every plant on the transects with flowers or fruits visible. We updated reproduction data for only a subset (n = 14) of the plants with flowers or fruits visible at Upper Table Rock. Due to a lack of plants with flowers or fruits at the second visit, we did not update reproduction data for the Denman Wildlife Prairie *R. austro-oreganus* population. The updated reproduction data was used in the analysis.

Statistical Analyses

We used several types of analyses to examine how site characteristics and climate interact to affect plant growth and reproduction. There were three types of variables: plant variables, edaphic variables, and climate variables. The latter two can be grouped together under the name "site variables." The variables used are:

- Plant variables
    - Biomass (weight per plant; g)
    - Reproduction (number of flowers and fruits per plant, where fruits were countable)
    - Density (number of plants per unit area; number/m^2)
    - Biomass density (total biomass per unit area; g/m^2)
    - Number of types of damage observed
- Edaphic variables
    - Elevation (m)
    - Soil depth (cm)
    - Soil pH
    - Total soil nitrogen (mg)
    - Total soil carbon (mg)

- Soil carbon:nitrogen ratio
- Bulk density (g/cm^3)
- Soil texture (sand, clay, and silt fraction; %)
- Ammonium (NH_4^+-N; $\mu g/cm^2$ per burial period)
- Nitrate (NO_3^--N; $\mu g/cm^2$ per burial period)
- Total plant available (inorganic) nitrogen (ammonium and nitrate; $\mu g/cm^2$ per burial period)

- Climate variables
  - Precipitation by season (mm)
  - Minimum temperature by season (°C)
  - Mean temperature by season (°C)
  - Maximum temperature by season (°C)
  - Dewpoint temperature by season (°C)

We used nonmetric multidimensional scaling (NMDS) to collapse the raw site variables (edaphic and climate) into fewer variables while avoiding the problems of multicollinearity (Beals 2006). NMDS is an ordination method that uses rank orders rather than Euclidean distances among variables; it is particularly useful when there are more variables than observations, as in this data set. We used the *metaMDS()* function in R's vegan package (Oksanen et al. 2015), with Bray-Kurtis dissimilarities and two dimensions. This function applies a square root transformation and Wisconsin double standardization, and then uses Principal Coordinate Analysis (PCA) to rotate the solution so that the first axis explains the greatest amount of variability.

We compared biomass and reproduction among sites for each species using one-way ANOVA and post-hoc Tukey tests. Where necessary, natural logarithm-transformed and square root-transformed data were used in these analyses to meet the underlying assumptions. In all cases, the reported means are back-transformed from the transformed data to the original units. Where data did not meet the underlying assumptions of ANOVA, we used a Kruskal-Wallis test instead.

We used Pearson correlations to determine if there is any correlation between the plant variables and the individual edaphic and climate variables as well as the NMDS axis scores, with a significance level of 0.10 for each correlation (non-directional test). We did this in two ways: (1) by species and (2) all populations combined by z-score standardizing biomass. Because the differences in the number of flowers produced by the four species was so disparate, reproduction was not included in the all species analysis.

By species correlations were done on the entire dataset for each species as well as by quartile based on biomass (e.g., only the smallest 25% of plants) to determine if the strength or direction of any relationship varied with plant size. By quartile correlations are only considered for reproduction and biomass; it is not meaningful to analyze density or biomass density in this way because these variables were calculated on whole population basis, rather than within each population (e.g., one single density number for each population). Furthermore, the results of by quartile correlations are only reported if they varied from the overall correlations. Finally, we used multiple linear regression to predict standardized biomass based on NMDS axis scores.

Results

Characterizing Site Variables

The NMDS ordination clearly grouped the populations by geographic location (Figure 21; stress = 0.050). Latitude was not included in the ordination, but latitude and the first NMDS dimension are strongly correlated (r = +0.802). Although there was no clear separation of variable type (edaphic vs. climate) along either axis, in general the edaphic site variables were stronger contributors to the axes than the climate variables. Clay fraction as by far the strongest contributor to the first axis, followed by total carbon and total nitrogen (Supplemental Figures 5 and 6; Supplemental Table 2). Nitrate was the strongest contributor to the second axis, closely followed by total inorganic nitrogen. Of the climate variables, precipitation (all seasons) had the strongest contribution, though it is at best an intermediate contribution. No measure of temperature in any seasons was an important contributor to either axis.

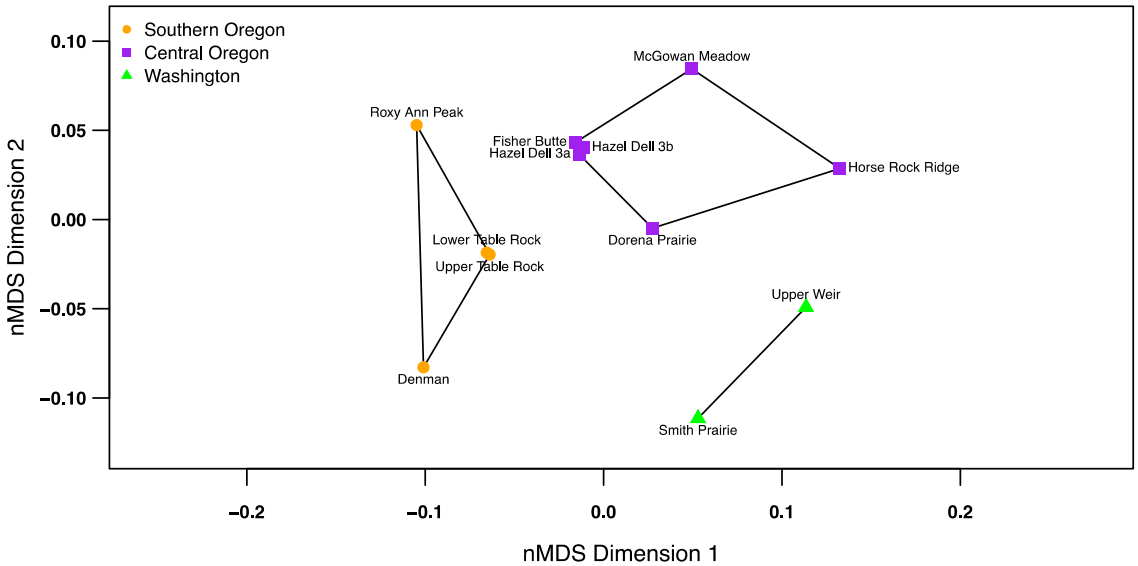


Figure 21. Nonmetric multidimensional scaling (NMDS) of site variables for all 12 populations. Different colors/shapes indicate the different region groupings; polygons connecting different populations indicate the groupings identified by the NMDS.

Allometric Equations

Ranunculus austro-oreganus

The allometric equation developed for *R. austro-oreganus* in 2010 (Fegan, unpublished) and modified for the data we collected ($r^2 = 0.873$) was:

$$\ln(Biomass) = -9.628 + (0.867 * \ln Leaf\ Area) + \left(0.726\sqrt{Number\ of\ Leaves}\right)$$

In this model, the area of the largest leaf is calculated as a circle based on the length of the largest leaf measured in the field. We then used this mode to calculate biomass for *R. austro-oreganus* populations.

Sidalcea malviflora ssp. virgata

The initial model we developed to model biomass for *S. malviflora* ssp. *virgata* included basal area (calculated as an ellipse based on the two largest perpendicular dimensions), the area of the largest leaf (calculated in the same way as *R. austro-oreganus*), and the number of leaves. However, because we did not count the number of leaves for all plants at all sites and could not find any combination of the other variables that adequately predicted the number of leaves in the training data set, this variable was dropped from the model. The resulting model had an r^2 value of 0.84 ($F(2,33) = 88.21$; $p < <0.001$):

$$Biomass = \left(-0.018 + \left(0.045\sqrt{Basal\ Area}\right) + (0.005 * Leaf\ Area)\right)^2$$

As was the case for number of leaves, basal area was not measured for all plants at all sites. In particular, it was not measured for plants with fewer than 6 leaves at Dorena Prairie and Hazel Dell 3a. However, in this case we were able to develop a model with an r^2 value of 0.66 relating basal area to other parameters ($F(1,194) = 236.1$; $p < <0.001$):

$$\ln(Basal\ Area) = 2.046 + (1.270 * \ln Number\ of\ Leaves) + (0.039 * Leaf\ Area) - (0.010 * Leaf\ Area * \ln Number\ of\ Leaves)$$

The values calculated from this equation were used where a basal area was not measured in the field to calculate biomass.

Microseris laciniata

Based on how biomass in the training data set was related to flowering status in *M. laciniata* (flowering plants tended to have higher biomass), two separate allometric equations were developed for this species: one for non-flowering plants and one for flowering plants.

For plants without flowers, basal area and the length of the longest leaf were important variables. However, we did not measure basal area at all sites and none of the possible models relating other variables to basal area had an acceptable r^2 value. Instead, we forced basal area out of model selection and obtained a model with length of the longest leaf, number of leaves, and number of grazed leaves ($r^2 = 0.69$; $F(3,11) = 8.26$; $p = 0.004$). However, when this model was applied to the full data set, the results were nonsensical. Returning to model selection yet again resulted in a model with a reduced r^2 value ($r^2 = 0.59$; $F(2,12) = 8.52$; $p = 0.005$), but reasonable values for biomass when applied to the full data set. The resulting model was:

$$Biomass = \left(-0.088 + (0.152 * \ln Remaining\ Leaves + 0.01) + (0.018 * Length\ of\ Longest\ Leaf)\right)^2$$

In this equation, the number of remaining leaves was calculated as the total number of leaves minus one half the number of grazed leaves, based on field observations of the amount of a leaf that is typically missing when leaves are grazed.

For plants with flowers, model development was simpler. All selection methods resulted in the same model, which had an r^2 value of 0.61 ($F(3,16) = 8.21$; $p = 0.001$). This model includes the number of remaining leaves (calculated in the same way as for plants without flowers), the number of flowers, and the height of the tallest stem:

$$\ln(Biomass + 0.01) = -2.320 + (0.372 * \ln Remaining\ Leaves + 0.01) + (0.576 * \ln Number\ of\ Flowers + 0.01) + \left(0.224 * \sqrt{Tallest\ Stem}\right)$$

Both of these equations were applied to data for the four *M. laciniata* populations.

Eriophyllum lanatum

For *E. lanatum*, one model was developed based on the entire training data set, which had a very high r^2 value of 0.97 ($F(3,1) = 210.4$; $p << 0.001$). This model included basal area, height of the tallest vegetative leaf, and the number of flower stalks:

$$Biomass = -6.079 + (0.615 * \ln Basal\ Area) + \left(0.753\sqrt{Height\ of\ Tallest\ Vegetative\ Leaf}\right) + (0.161 * Number\ of\ Flower\ Stalks)$$

This equation was applied to data for the six *E. lanatum* populations.

Demographic Censuses—Biomass and Reproduction

Biomass varied considerably among all three *R. austro-oreganus* populations when biomass was log-transformed to account for positive skewness (Figure 22; $F(2, 646) = 62.73$; $p << 0.01$). In fact, mean plant biomass at Denman was twice as large as mean plant biomass at Roxy Ann Peak.

Mean reproduction (number of flowers) per flowering plant also differed among the three populations when data were square root transformed (Figure 22; $F(2, 172) = 5.08$; $p = 0.007$), although reproduction only differed significantly between Denman and Upper Table Rock. However, the proportion of the population surveyed that

was flowering at the time of the census varied by site (16% at Roxy Ann Peak; 26% at Denman; 35% at Upper Table Rock), and it is unclear if this was due to true differences in flowering or an artifact of not doing the census at exactly the same phenological point for each population.

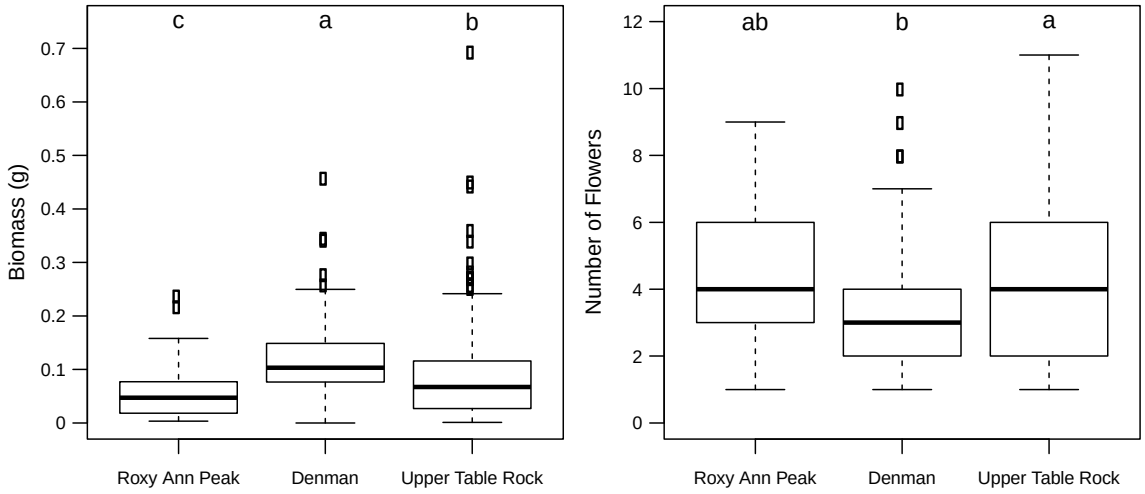


Figure 22. Boxplots of biomass (all plants) and reproduction (only flowering plants) for the three *R. austro-oreganus* populations. Different letters indicate significant differences among sites ($p < 0.05$).

For *S. malviflora* ssp. *virgata*, biomass was significantly different among all three populations when biomass was log transformed (Figure 23; $F(2, 537) = 31.04$; $p << 0.001$). On average, *S. malviflora* ssp. *virgata* plants are over twice as big at Dorena Prairie as they are at Hazel Dell 3a.

At all sites, there were many more non-reproductive plants than plants with flowers or fruits. The proportion of reproductive plants was lowest at McGowan Meadow at 13.0% and highest at Dorena Prairie at 27.5%; 17.2% of plants at Hazel Dell 3a had flowers and/or fruits. The number of flowers and fruits per reproductive plant varied among the sites ($F(2, 109) = 4.60$; $p = 0.01$). However, only Dorena Prairie and Hazel

Dell 3a significantly differed. Additionally, Dorena Prairie had a number of plants with exceptionally large numbers of fruits and flowers.

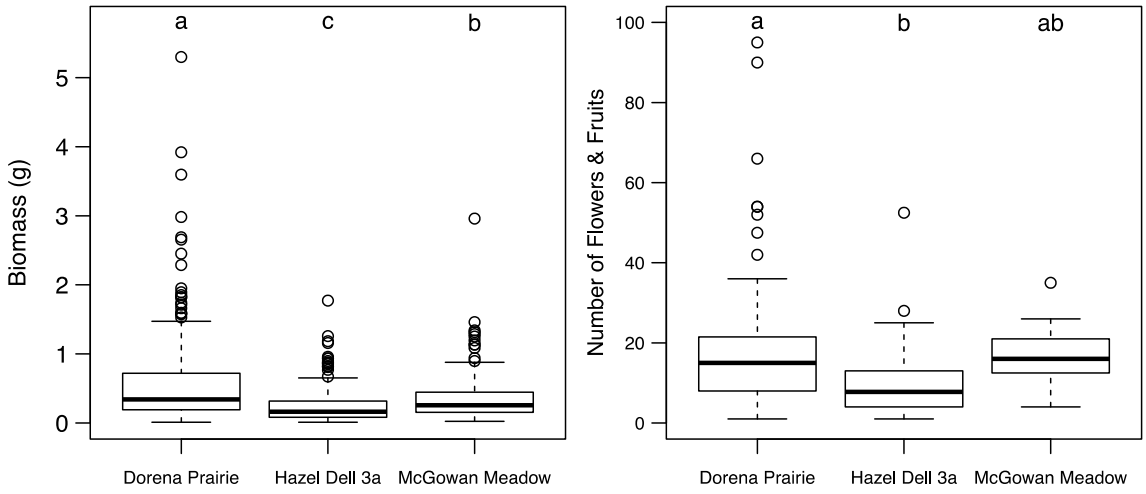


Figure 23. Boxplots of biomass (all plants) and reproduction (only flowering plants) for the three *S. malviflora* ssp. *virgata* populations. Different letters indicate significant differences among sites ($p < 0.05$).

Again, sites differed in biomass for *M. laciniata* (Figure 24; $F(3, 805) = 71.48$; $p << 0.001$). Mean biomass at Fisher Butte was over twice as high as that at Upper Weir, the site with the second largest plants. While the differences in mean biomass among Upper Weir and the other two sites were not as great, mean biomass was smaller at Lower Table Rock and Hazel Dell 3B ($p < 0.05$). However, mean biomass was not different among these two sites ($p > 0.05$).

In addition to being much larger, plants at Fisher Butte had more flowers and a greater proportion of the population was flowering (62%, vs. 17% at Lower Table Rock, 26% at Hazel Dell 3b, 31% at Upper Weir). (Figure 24; Kruskal-Wallis test; $\chi^2(3) = 161.56$, $p << 0.001$). The majority of flowering plants at this population had two or more flowers (83%), and as many as 18 flowers were observed on a single plant. In the other three populations, over half of the plants with flowers present only had one flower

and the greatest number of flowers on a single plant was 4 (Lower Table Rock and Hazel Dell 3b) or 3 (Upper Weir). Furthermore, these populations had many fewer flowering plants, with at most 31% of the surveyed plants in flower (Upper Weir).

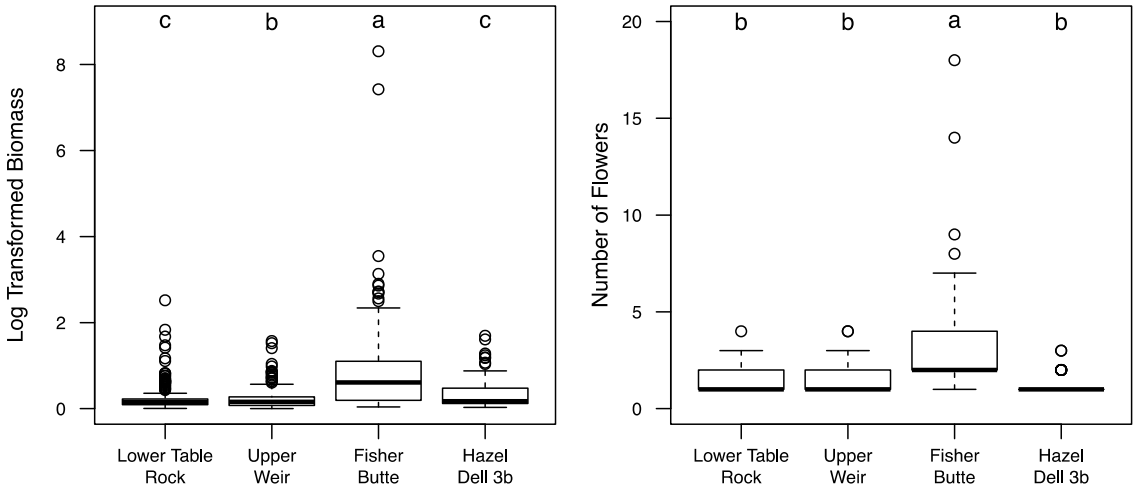


Figure 24. Boxplots of biomass (all plants) and reproduction (only flowering plants) for the four *M. laciniata* populations. Different letters indicate significant differences among sites ($p < 0.05$).

For *E. lanatum*, there were also significant differences in log-transformed mean biomass among populations (Figure 25; $F(5, 1189) = 19.50$, $p < 0.05$). Mean biomass at Denman, Fisher Butte, and Smith Prairie was ~4-fold higher (0.40 – 0.52 g/ plant; back transformed means) than plants at Upper Table Rock, Horse Rock Ridge, and Upper Weir (0.13 – 0.18 g/plant; back transformed means; $p < 0.05$).

The proportion of plants that were flowering varied from a low of 13% (Horse Rock Ridge to a high of 57% (Fisher Butte; see Table 8). Additionally, there was considerable variation in mean reproduction for the six *E. lanatum* population (Figure 25; $F(5, 463) = 5.56$; $p << 0.001$). The mean number of flowers at Denman was more than three times the mean number of flowers at Horse Rock Ridge (8.5 flowers vs. 2.6 flowers; back-transformed). A single plant at Denman produced 253 flowers, which is

more than twice as many flowers produced by a single plant at any other population. In fact, reproduction at Denman was significantly different than Fisher Butte, Horse Rock Ridge, and Smith Prairie; Horse Rock Ridge was also significantly different than Upper Table Rock and Upper Weir (Figure 25; $p < 0.05$). None of the other sites differed from one another ($p < 0.05$).

Table 7. Proportion of plants surveyed that were flowering at the time of census for *E. lanatum* populations.

Site	Plants Flowering (%)
Smith Prairie	53
Upper Weir	27
Horse Rock Ridge	13
Fisher Butte	57
Upper Table Rock	41
Denman	40

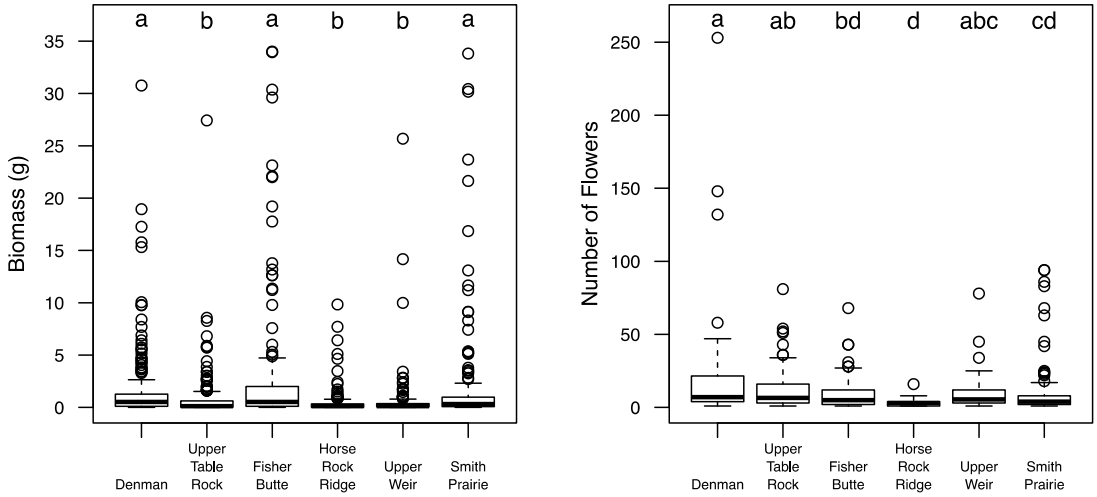


Figure 25. Boxplots of biomass (all plants) and reproduction (only flowering plants) for the six *E. lanatum* populations. Different letters indicate significant differences among sites ($p < 0.05$). Note that plants larger than 35 g are not shown here (see Supplemental Figure 7 for full boxplot with all plants included).

Correlations among Plant, Edaphic, and Climate Variables

Ranunculus austro-oreganus

In general, the direction and strength of the correlation of seasonally measured climate variables with both reproduction and biomass for *R. austro-oreganus* was

consistent across seasons for each variable, with the exception of minimum temperature (see below); for brevity, all other variables have been collapsed into annual values here for this species (Figure 26; Supplemental Figure 8).

Reproduction and biomass were positively correlated for *R. austro-oreganus*; bigger plants tended to have more flowers and fruits (r = +0.46; Figure 26; Supplemental Figure 8). Biomass and both density measures were negatively correlated with moderately weak strength (r = -0.29 for density; r = -0.24 for biomass density); when density was lower the plants tended to be larger, though this was not a strong relationship. Reproduction was only weakly correlated with density measures (r = -0.12 for density; r = -0.14 for biomass density)

Reproduction was not strongly correlated with any of the edaphic or climate variables for *R. austro-oreganus*; the variables most strongly correlated with reproduction were silt fraction and total carbon (r = +0.19 for both). While the magnitude of the correlation with reproduction was similar for all edaphic variables ($0.19 > r > 0.11$ and $-0.11 > r > -0.19$) excepting total inorganic nitrogen and nitrate, the only climate variables with correlations of similar magnitude were minimum winter temperature (r = -0.18) and minimum summer temperature (r = -0.14). Furthermore, there was no consistent pattern regarding the direction of the correlation across either the climate or edaphic variables. Reproduction was weakly correlated with the first NMDS axis (r = + 0.19) and not correlated with the second axis (r = -0.02).

Correlations among edaphic and climate variables and biomass were stronger than those for reproduction. The edaphic variables with the strongest correlations with biomass were total inorganic nitrogen and nitrate (r = +0.39 and r = +0.38, respectively).

However, in general the correlations among biomass and climate variables were stronger than the correlations among biomass and edaphic variables ($|r| \sim 0.3$ for climate variables). Although bulk density ($r = +0.34$), elevation ($r = +0.33$), N:C ratio ($r = +0.33$), and soil depth ($r = -0.24$) were correlated with a similar strength, all other physical variables were weakly correlated ($|r| < 0.12$). Of the climate variables, minimum spring temperature was most strongly correlated with biomass ($r = +0.38$). Again, there was no consistent pattern regarding the direction of the correlation across either the climate or edaphic variables. Finally, the correlation between biomass and the second NMDS axis was moderately strong ($r = -0.40$); the first NMDS axis was very weakly correlated with biomass ($r = -0.06$).

It was interesting to note that the variables that were most strongly correlated with reproduction were much more weakly correlated with biomass, and vice versa. Furthermore, the direction of the correlation was in most cases reversed. For example, total inorganic nitrogen and nitrate had moderate, positive correlations with biomass, but only nitrate was significantly correlated with reproduction and the correlation was weak ($r = -0.07$).

When the data were split into quartiles by biomass, the correlations among reproduction and edaphic variables were clearly stronger than the correlations among reproduction and climate variables for larger plants; the difference was particularly pronounced for the largest 25% of plants (Supplemental Figure 9). For these plants, the magnitude of the correlation between every edaphic variable—except for soil depth—and reproduction was greater than 0.33 or less than -0.27. Yet, even the strongest of these correlations was still only moderately strong (reproduction and N:C ratio; $r = -0.40$).

Furthermore, the direction of the correlation varied within each variable type. No variable had a correlation greater than |0.17| for biomass.

Visual analysis of the spatial distribution of plants in the *R. austro-oreganus* populations suggested that there were strong differences in density among the populations (Supplemental Figure 10). Both measures of density for *R. austro-oreganus* were strongly correlated ($r < 0.62$ or > 0.75) with most of the edaphic variables with a similar magnitude and direction (Figure 26). Soil depth and soil pH were particularly strongly correlated with both measures of density ($r = +0.99$ for soil depth and both measures of density; $r = +0.86$ for soil pH and plant density; $r = +0.92$ for soil pH and biomass density). The exceptions were nitrate and total inorganic nitrogen, which showed modest correlations with density and biomass density ($+0.51 \geq r \geq +0.34$) and weak correlations with N:C ratio and bulk density ($+0.04 \geq r \geq -0.26$). All climate variables were also very strongly correlated with both measures of density ($r \geq +0.78$). Furthermore, both NMDS axes were strongly correlated with density, and the second axis was more strongly correlated for both measures of density ($r = +0.82$ for plants/m^2; $r = +0.72$ for biomass/m^2). Correlations with density and the first axis were slightly weaker ($r = +0.56$ for plants/m^2; $r = +0.67$ for biomass/m^2). Interestingly, the direction of the correlations between density and the site variables was opposite that of the correlations between biomass and site variables, and the variables that were most strongly correlated with biomass have some of the weakest correlations with density.

The number of types of damage experienced by plants was not strongly correlated with any other variable for *R. austro-oreganus*.

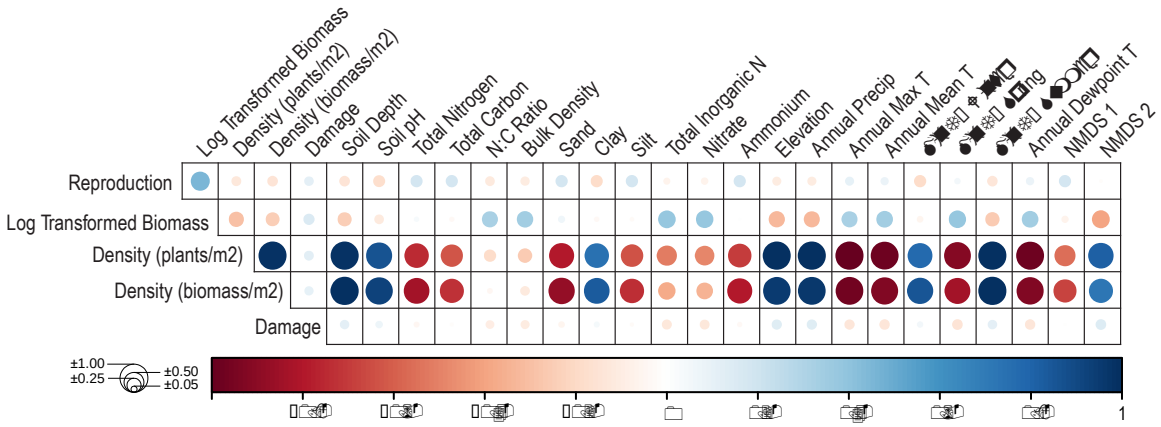


Figure 26. Table of all correlations for plant, edaphic, and climate variables for *R. austro-oreganus*. The size of the circle and the intensity of the color represent the strength of the correlation (smaller and lighter = weaker, larger and darker = stronger); blue indicates a positive correlation and red indicates a negative correlation. The value of each correlation is shown in Supplemental Figure 8. Additionally, note that biomass was log transformed and only minimum temperature is shown separated by season due to the lack of difference among seasons for other climate variables.

Sidalcea malviflora ssp. virgata

For *S. malviflora* ssp. *virgata*, the direction and strength of the correlations of seasonally measured climate variables with both reproduction and biomass were consistent across seasons; for brevity, these variables have again been collapsed into annual values here for this species (Figure 27; Supplemental Figure 11).

Biomass and reproduction were moderately positively correlated; larger plants had more flowers and fruits for *S. malviflora* ssp. *virgata* (r = +0.43). The correlation between biomass and density was weak (r = +0.04), whereas the correlation between biomass and biomass density was moderate (r = +0.23). Reproduction was weakly correlated with density (r = +0.10) and weakly correlated with biomass density (r = +0.17).

The correlations among site variables and both reproduction and biomass were even weaker for *S. malviflora* ssp. *virgata* than for *R. austro-oreganus.* In fact, few edaphic variables and none of the climate variables had a correlation with reproduction

stronger than |0.07|. Of these variables, soil depth was the strongest, and it was only weakly correlated (r = +0.18).

Biomass was most strongly correlated with nitrate (r = -0.32), soil depth (r = -0.25), and then N:C ratio (r = -0.24) for *S. malviflora* ssp. *virgata*. None of the climate variables had an absolute correlation greater than 0.13. The first NMDS axis was moderately correlated with biomass at r = +0.26; the second axis was weakly correlated (r = -0.13).

Again, visual analysis of the spatial distribution of plants in the *S. malviflora* ssp. *virgata* populations suggested that there were strong differences in density among the populations (Supplemental Figure 12). Density was much more strongly correlated with site variables than was biomass or reproduction for *S. malviflora* ssp. *virgata*. In contrast to *R. austro-oreganus*, for this species there were clear differences in the strength of the correlations between the two density measurements and the site variables. The strongest correlations with edaphic variables were with biomass density (soil depth, r = -1.00; soil pH, r = +1.00; sand fraction, r = +1.00; silt fraction, r = -0.94; ammonium, r = +1.00), but density as plants/m^2 was always more strongly correlated with the climate variables (|r| > 0.87). However, with the exception of nitrate, every site variable was strongly correlated with density (|r| > 0.57). Therefore, it is inconclusive whether climate or edaphic site variables affected either density measure more strongly. Although the relative strength of the correlations between the two density measures and site variables varied, the direction was always the same. Furthermore, it was usually in the opposite direction of the correlation between biomass and site variables; the exceptions were soil pH, sand fraction, silt fraction, and ammonium. The latter four were also among the

edaphic variables that were most strongly correlated with biomass density. The second NMDS axis was strongly negatively correlated with both density measures, though not as strongly as some individual site variables (density, r = -0.95; biomass density, r = -0.93). Although the first axis was also strongly negatively correlated with density (r = -0.53), it was only weakly and positively correlated with biomass density (r = +0.12).

For *S. malviflora* ssp. *virgata*, all temperature variables (maximum, mean, and minimum temperatures) were positively correlated with both density measures; sites with warmer temperatures tend to have more plants and more biomass per area. Precipitation was negatively correlated with both density measures; sites with more precipitation tend to have smaller and fewer plants. This was the opposite of what was observed for *R. austro-oreganus*, which has its range in the hotter and drier climate of Southern Oregon.

Again, the number of kinds of damage experienced by plants was not strongly correlated with any other variable, though it was moderately correlated with biomass (r = +0.24).

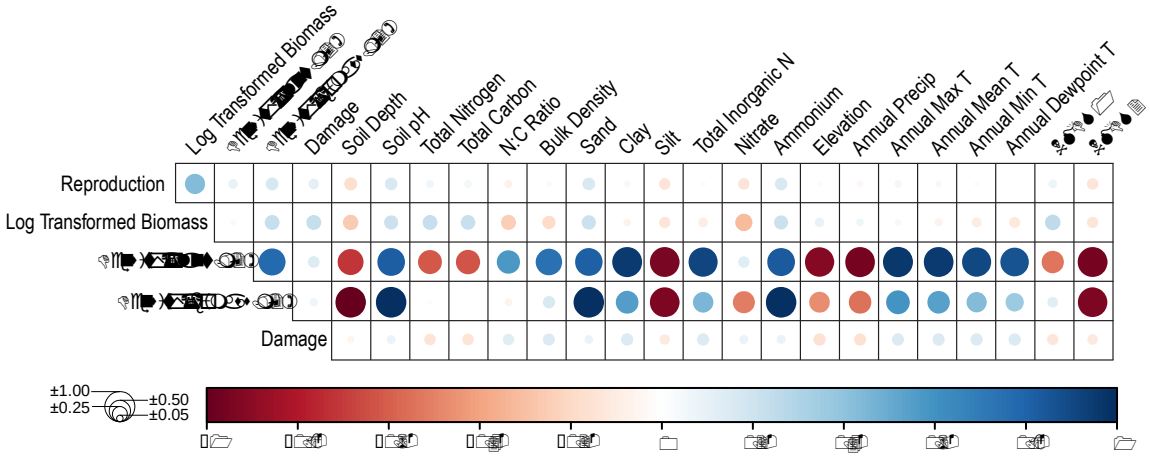


Figure 27. Table of all correlations for plant, edaphic, and climate variables for *S. malviflora* ssp. *virgata*. The value of each correlation is shown in Supplemental Figure 11. Additionally, note that biomass was log transformed and annual correlations are shown for all climate variables due to the lack of difference among seasons.

Microseris laciniata

For *M. laciniata*, the correlations between reproduction and biomass and most seasonally measured climate variables had different directions and magnitudes across seasons. The exceptions were max temperature and dewpoint temperature; for brevity, these two variables have been collapsed into annual values for this species. The other climate variables remain separated by season (Figure 28; Supplemental Figure 13).

Reproduction and biomass were strongly correlated for *M. laciniata* ($r = +0.78$; both density measures and biomass were also positively correlated, but more weakly ($r = +0.43$ for plants/m^2; $r = +0.46$ for biomass density). Similarly, reproduction was moderately correlated with both density measures ($r = +0.44$ for plants/m^2; $r = +0.45$ for biomass density).

Of the edaphic variables, nitrate, silt fraction, and N:C ratio were the most strongly correlated with reproduction ($0.36 \geq |r| \geq 0.37$). Of the climate variables, spring and winter minimum temperature and dewpoint temperature (r from 0.30 to 0.33). There were few patterns in the direction of the correlation with reproduction within either the edaphic or climate variables. Again, the second NMDS axis was moderately negatively correlated with reproduction ($r = +0.30$), though the first axis was very weakly negatively correlated ($r = -0.05$).

Soil pH was the edaphic variable most strongly correlated with biomass ($r = +0.36$), followed by N:C ratio ($r = +0.34$), nitrate, and ammonium ($r = -0.29$ for both). Again, most climate variables were generally less strongly correlated with biomass for *M. laciniata*. The correlation with minimum spring temperature was the strongest climate variable–biomass correlation ($r = +0.31$). Precipitation was moderately positively

correlated with biomass, with winter precipitation being the strongest seasonal correlate (r = +0.23). Although none of the correlations were strong, edaphic variables were generally more strongly correlated with biomass than climate variables were. The correlation of biomass with the second NMDS axis, composed primarily of edaphic variables, was moderately weak at +0.20. though the direction of the correlations with each variable was the same for both reproduction and biomass. Furthermore, although the most strongly correlated variables were different for reproduction and biomass, the magnitude of the correlations was similar for most variables.

As in *R. austro-oreganus* and *S. malviflora* ssp. *virgata*, visual analysis of the spatial distribution of plants in the *M. laciniata* populations suggested that there were differences in density among the populations (Supplemental Figure 14). Density was generally more strongly correlated with site variables than either biomass or reproduction for *M. laciniata*. Correlations with the two density measures had similar magnitudes and were always in the same direction, but density was slightly more strongly correlated with the site variables than biomass density for most site variables. Similar to reproduction, the edaphic variables most strongly correlated with density were nitrate (r = -0.89) and silt fraction (r = +0.89). Interestingly, although silt fraction and sand fraction were also strongly correlated with density (r = -0.68 and r = +0.89, respectively), the correlation with clay was nearly 0. Climate variables were not as strongly correlated with density as the edaphic variables, but the correlations were still strong. The strongest correlations were with minimum temperature (winter: r = +0.704; spring: r = +0.68; summer: r = -0.65) and dewpoint temperature (r = +0.68). Density increased with more precipitation in the winter (r = +0.48), but was unrelated to summer precipitation

(r = +0.01). As with the previous two species, the second NMDS axis was strongly correlated with both measures of density (r = +0.76 for density; r = +0.64 for biomass density). In contrast, the first axis was moderately to weakly negatively correlated with density (r = -0.25 for density; r = -0.17 for biomass density).

In contrast to *R. austro-oreganus* and *S. malviflora* ssp. *virgata*, the number of types of damage experienced by *M. laciniata* plants was moderately correlated with a number of site variables. Total inorganic nitrogen, sand fraction, minimum summer temperature and mean winter temperature were the strongest correlates with damage types (r = -0.37 for inorganic nitrogen, sand fraction, and minimum summer temperature; r = +0.37 for mean winter temperature). More edaphic variables were moderately correlated with damage types than were climate variables.

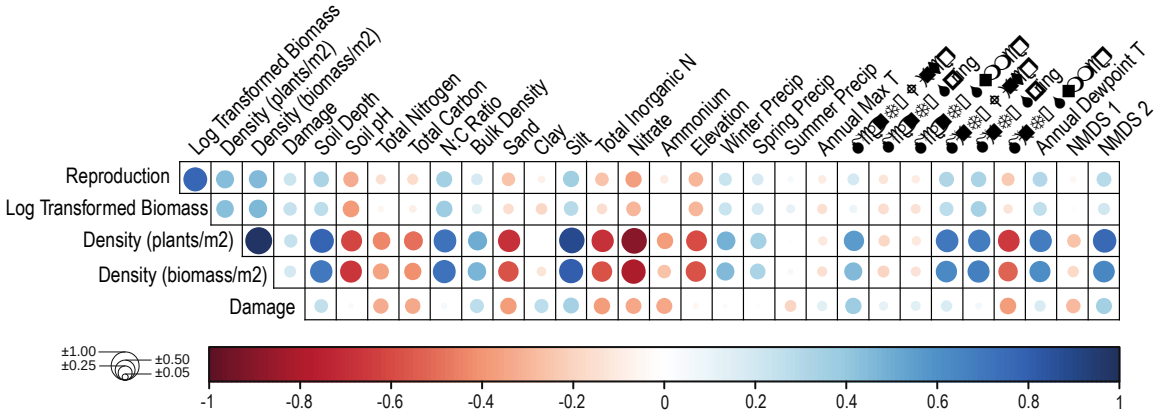


Figure 28. Table of all correlations for plant, edaphic, and climate variables for *M. laciniata*. The value of each correlation is shown in Supplemental Figure 13. Additionally, note that biomass was log transformed and annual correlations are shown for all climate variables due to the lack of difference among seasons.

Eriophyllum lanatum

For *E. lanatum*, the correlation among reproduction and biomass and most seasonally measured climate variables had different directions and magnitudes across seasons. However, for maximum temperature and dewpoint temperature the magnitudes

and directions were consistent across seasons; for brevity, these two variables have been collapsed into annual values for this species. The other climate variables remain separated by season (Figure 29; Supplemental Figure 15).

Biomass and reproduction were strongly positively correlated for *E. lanatum* ($r = +0.63$). Biomass was very weakly correlated with density ($r = +0.08$) and was not significantly correlated with biomass density. Reproduction was not significantly correlated with either measure of density.

The correlations between all site variables and biomass and reproduction were much weaker for this widespread species than for the other three species ($|r| \leq 0.18$). Neither NMDS axis was even moderately correlated with either biomass or reproduction.

Although less obvious than in the other species, visual analysis of the spatial distribution of plants in the *E. lanatum* populations suggested that there were differences in density among the populations (Supplemental Figures 16 and 17). A few site variables were strongly correlated with density for *E. lanatum*. Unlike the other three species, there was major variation in the strength of the correlation between an individual site variable and the two density measures; moreover, edaphic variables tend to be more strongly correlated with the density, and climate variables tend to be more strongly correlated with biomass density. The strongest correlations were between nitrate and total inorganic nitrogen and number of plants/m^2 ($r = +0.76$). Silt fraction was the only other site variable that was strongly correlated with number of plants/m^2 ($r = -0.66$). Biomass density increased with minimum temperature in all seasons ($r = +0.76$ to $+0.80$). Additionally, biomass density decreased with maximum temperature ($r = -0.70$). Density was also strongly correlated with the second NMDS axis ($r = -0.66$ for density; $r = -0.70$

for biomass density), and again the correlations with the first NMDS axis were much weaker and in the opposite direction (r = +0.16 for density; r = +0.41 for biomass density). The number of kinds of damage was moderately positively correlated with biomass and reproduction (r = +0.36 and r = +0.25, respectively), and weakly correlated with minimum temperature in all seasons (spring and summer: r = +0.19; winter: r = +0.16).

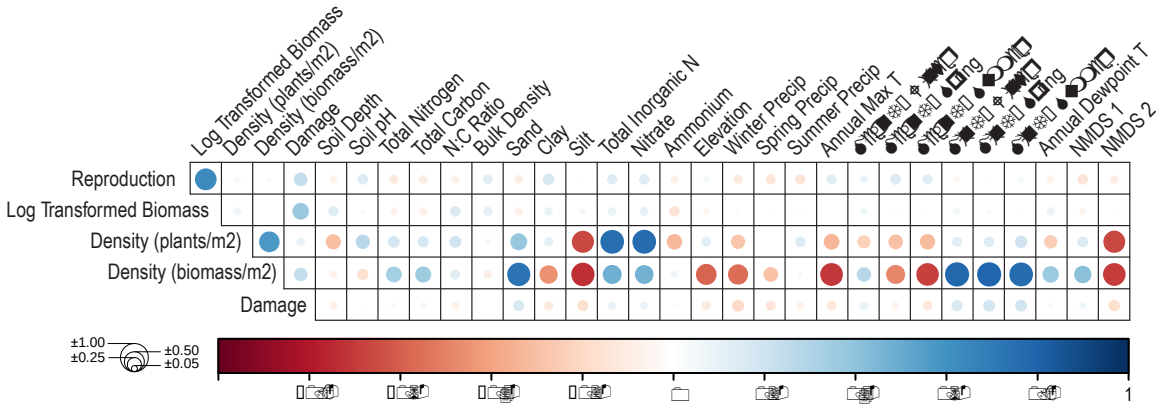


Figure 29. Table of all correlations for plant, edaphic, and climate variables for *E. lanatum*. The value of each correlation is shown in Supplemental Figure 15. Additionally, note that biomass was log transformed and annual correlations are shown for all climate variables due to the lack of difference among seasons.

All Species

When all sites of all species were combined, standardized biomass was not significantly correlated with any site variable or either NMDS axis (30; Supplemental Figure 18). A linear model relating standardized biomass and the two NMDS axes has very low explanatory power; only 1% of the variation in biomass was explained by the model ($F(2, 3189) = 11.03$; $p << 0.001$). Surprisingly, biomass and both measures of density were not significantly correlated.

Both measures of density were correlated with very few site variables, but there were strong correlations with a few variables. Number of plants/m^2 was strongly

positively correlated with elevation (r = +0.70), followed by dewpoint temperature in all seasons (winter: r = -0.65; spring; r = -0.61; summer: r = -0.59). Minimum temperature (all seasons) was moderately positively correlated with biomass density; winter minimum temperature was the most strongly correlated season (r = +0.58). However, when we more closely examined these correlations, it was clear that they were strongly influenced by three outlier populations: *E. lanatum* at Smith Prairie, *E. lanatum* at Denman, and *R. austro-oreganus* at Roxy Ann Peak (Figure 31). Biomass density was over 60 times greater at Smith Prairie than it is at Denman, which was itself over 15 times greater than the site with the next highest biomass density. Density at Roxy Ann Peak was over 5 times greater than the site with the next highest density. When these outlier sites were removed from the dataset, the correlations changed somewhat (Figure 32; Supplemental Figure 19). Minimum temperature in all seasons was instead moderately negatively correlated with density (winter: r = -0.49; spring; r = -0.46; summer: r = -0.53); only minimum summer temperature remained correlated with biomass density, and the direction of the correlation switched (r = -0.51). Although density still increased with elevation, the relationship was not as strong (r = +0.46). Two additional edaphic variables were moderately positively correlated with density: total inorganic nitrogen (r = +0.47) and nitrate (+0.49). For biomass density, the only climate variables in addition to minimum summer temperature that was significantly correlated were winter precipitation (r = +0.53) and spring precipitation (r = +0.46). Soil pH (r = -0.51) and carbon to nitrogen ratio (r = +0.69) were also significantly correlated with biomass density.

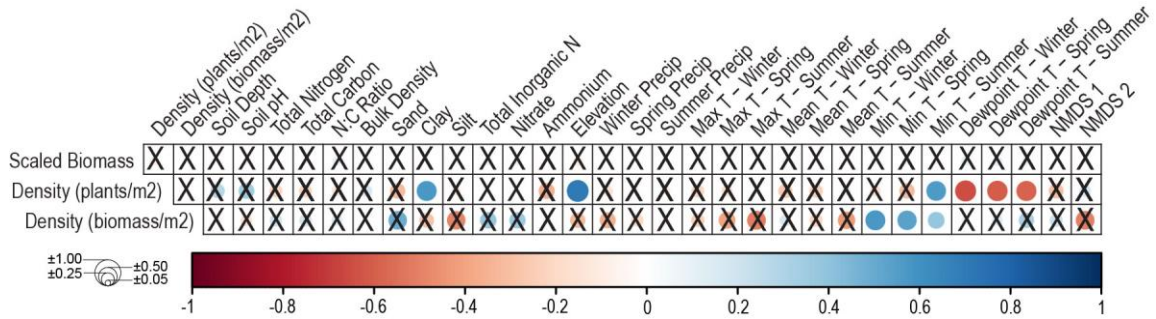


Figure 30. Table of correlations for standardized biomass, edaphic, and climate variables for all species. Correlations that were not significant are marked with an "X." The value of each correlation is shown in Supplemental Figure 18.

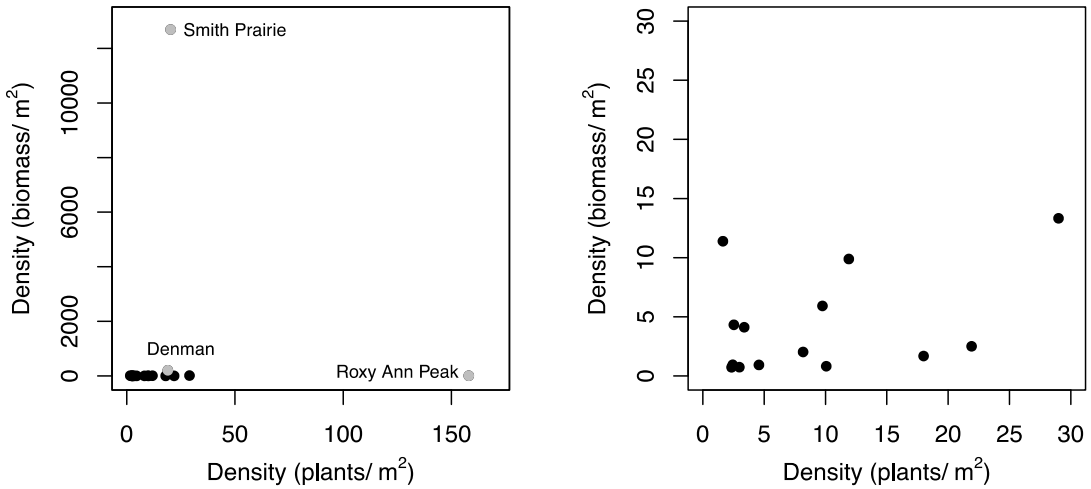


Figure 31. Comparison of density and density biomass for each population. The left figure shows all populations, with outliers colored in grey and named. The right figure shows only the 13 populations that remain when the outliers are removed.

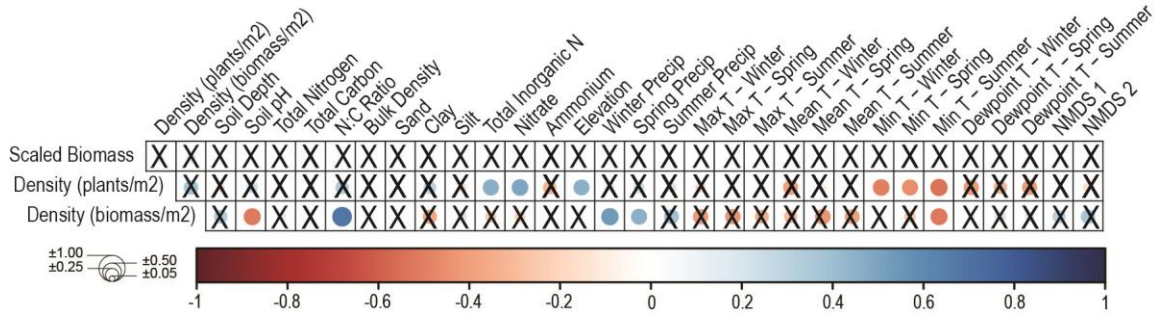


Figure 32. Table of correlations for standardized biomass, edaphic, and climate variables for all species with outliers (*E. lanatum* populations at Smith Prairie and Denman and *R. austro-oreganus* at Roxy Ann Peak) removed. Correlations that were not significant are marked with an "X." The value of each correlation is shown in Supplemental Figure 19.

Discussion

Understanding how plants respond to edaphic and climatic factors is critical to predicting how they might react to future climate conditions in a changing world. The response of prairies and grasslands throughout the world to climate change has been studied extensively (e.g. Swift et al. 1998, Grime et al. 2000, Booth et al. 2005, Adler and HilleRisLambers 2008, Wang et al. 2014, Zelikova et al. 2014). However, much of the literature is focused on mid-continental prairies, which are different from the Mediterranean prairies of the Pacific Northwest in climate as well as biotic composition (Pfeifer-Meister and Bridgham 2007). Several studies have focused on prairies in Mediterranean climates and how climate versus edaphic factors influence response to simulated warming and altered precipitation regimes (e.g., Lloret et al. 2004, Fernandez-Going et al. 2012, Fernandez-Going and Harrison 2013, Pfeifer-Meister et al. 2013, 2015, Wang et al. 2014), but natural populations of species native to these prairies have not been as extensively studied.

Ordination of climate and edaphic variables clearly distinguished among the three different regions included in this study (southern Oregon, central Oregon, and Washington). Surprisingly, edaphic variables were the strongest contributors to both axes (Supplemental Figure 5; Supplemental Table 2), despite the fact that our study was designed to take advantage of the overall natural climate gradient paralleling the latitudinal gradient throughout the Pacific Northwest and there were major differences in soil characteristics within each region. This may reflect the nonrandom distribution of remnant populations of these species; it is also likely reflective of the inevitable overlap

between regional-scale geological processes that are important in the pedogenesis of soil and differences in climate.

For all species there were significant differences among two or more of the sites for both reproduction and biomass; furthermore, for each species, two sites with nearly identical climate conditions had significantly different biomass (Upper Table Rock and Denman for *R. austro-oreganus* and *E. lanatum*; Hazel Dell 3a and Dorena Prairie for *S. malviflora* ssp. *virgata;* Fisher Butte and Hazel Dell 3b for *M. laciniata*). However, no clear explanations for these significant differences emerged when the site variables were individually assessed, and neither edaphic or climate variables clearly dominated. Even in the case of *E. lanatum*, where field observations implied that the two significantly different groups of sites by biomass (Figure 25) were separated by soil texture, none of the soil texture measures (sand, silt, and clay fraction) were even moderately correlated with biomass. In general, reproduction and biomass were at best moderately correlated with site variables, and the species were idiosyncratic. Density instead emerged as much more strongly related with site variables.

In regards to our hypothesis concerning biomass and reproduction, the relationships between plant and site variables were generally not as expected for the populations surveyed in this study. Our data provided very little support for our hypothesis that edaphic variables would be the primary control over biomass and reproduction in these species. However, neither was there strong evidence that climate was a more important control over biomass and reproduction. In all species, the magnitude of the strongest correlation between biomass and either edaphic or climate variables was similar, and in all cases these are at best moderate correlations.

Furthermore, there were no consistent patterns among species. This is in contrast to the findings of Pfeifer-Meister et al. (2013) that plants consistently produced more biomass when subjected to artificial heating as well as supplemental precipitation, and that plant size was positively correlated with nitrogen availability for most species. However, Pfeifer-Meister et al. (2013) do note that nutrient availability increased with heating in their study, and this indirect effect may be responsible for increased plant biomass in heated plots. This pattern was not observed in our natural populations; warmer populations did not have greater nutrient availability. This was not surprising, as nutrient availability is controlled by a multitude of factors in addition to temperature (e.g., pH and soil type; Brady and Weil 2004). Moreover, nutrient availability (plant available nitrogen, as ammonium, nitrate, and total inorganic nitrogen) was only weakly to moderately correlated with biomass in our populations and the direction of the correlation was not consistent.

It is important to note that the strongest correlations among biomass, reproduction and site variables (both edaphic and climate) were for the species with only three or four populations (*R. austro-oreganus*, *S. malviflora* ssp. *virgata*, and *M. laciniata*). This limitation of our study design reflected the reality that these native species are geographically limited and occur within few places within their range because of large habitat losses and degradation (Bachelet et al. 2011). When the number of populations was increased to six with *E. lanatum*, there were no significant correlations between biomass and site variables and a few weak correlations between reproduction and site variables. This is not surprising, given that this species is widespread and can establish and persist under a variety of edaphic and climatic conditions. However, it is also

possible that the disparity in correlation strength could be due to our sampling design. Despite the fact that we censused approximately 200 plants in each population, there is effectively only one sample of each site variable for each population. In other words, there are only three samples for each site variable for *R. austro-oreganus* and *S. malviflora* ssp. *virgata*, only four samples for each site variable for *M. laciniata*, and six samples for each site variable for *E. lanatum.* It is possible that the stronger correlations within the species with fewer populations are an artifact of the very low sample size and the particular populations selected for this study. While individual species analysis is still useful, the results of the all-species analysis are likely more reliable and indicative of the response of Pacific Northwest prairie communities in general due to increased statistical power.

When we analyzed all 16 populations together, biomass was not correlated with any of the variables that we measured. Although six of these 16 populations are of a widespread species (*E. lanatum*), this is less than half of the populations included; it seems unlikely that the *E. lanatum* populations as a group were driving the lack of correlation, and there truly is no meaningful relationship between biomass of individual plants and site variables. Even when the three outlier populations were removed—two of which were *E. lanatum* populations—there was no correlation between biomass and any site variable. This is consistent with the findings of many other studies that species response at the local level is idiosyncratic, even within a single species (e.g., Parmesan and Yohe 2003, Lloret et al. 2004, Penuelas et al. 2007, Doak and Morris 2010, Corlett and Westcott 2013, Rumpf et al. 2014).

One particularly surprising result of this analysis was that biomass and density were not correlated across all 16 populations; this was true for both measures of density (plants/m^2 and biomass/m^2), and remained true when the three outlier populations were removed. This is in contrast to the theory of density-dependent mortality, or self-thinning—which has been supported in numerous studies—which posits that the growth of some plants will inevitably result in the death of others due to size-asymmetric competition for resources (Schwinning and Weiner 1998, Weiner et al. 2001, Stoll et al. 2002). Simply put, larger plants are disproportionately stronger competitors for resources than smaller plants under size-asymmetric competition. As a corollary to the process of self-thinning, increases in population biomass should be accompanied by a decrease in the number of plants (Stoll et al. 2002); this was not supported by our data, either, as density and biomass density were uncorrelated when all populations were included and positively correlated when the three outlier populations were removed. This could imply that competition was size-symmetric in these communities; under this scenario, self-thinning only occurs at very high densities, and all individuals are equally impacted by competition (Stoll et al. 2002). However, we only considered the species of interest at each site during our data collection, and thus have no way to assess how other members of the plant community could be affecting our results through interspecific competition or facilitation. Nor did we quantify the amount of damage—only the number of kinds—preventing us from effectively assessing how that could have affected these species. Recently, a number of studies have shown the importance of the biotic context in understanding how populations of the same species differ among sites, and have even postulated that the unexplained variance in range shifts can be attributed to biotic

interactions (Chen et al. 2011, Grassein et al. 2014, Eskelinen and Harrison 2015). It is entirely possible that different competitive environments due to a different suite of species present at each site could help to explain the differences among populations. For example, Grassein et al. (2014) observed that biomass production was greatest at the sites where the species of interest was dominant when compared to populations located near distribution limits. Anecdotally, we noticed that plants tended to be smaller when the overall site biomass seemed higher, but we have no way to rigorously investigate this observation with our data.

In contrast to the results of correlations among biomass, reproduction, and site variables, both measures of density (plants/m^2 and biomass/m^2) exhibited moderate to strong relationships with site variables. As all four of the species of interest are perennials, density is likely a much better measure of long-term processes and site history than either reproduction or biomass in a single year, and consequently may be a stronger indicator of demographic processes for these species. As previously discussed, the strong correlations among site variables and both density measures for *R. austro-oreganus* and *S. malviflora* ssp. *virgata* are particularly suspect due to the fact that only three sites of each were assessed and we were effectively trying to perform correlation analysis with only three observations. However, strong correlations were observed for *M. laciniata* and *E. lanatum*, as well as the cross-species analysis. We were still unable to say categorically say that either climate or edaphic variables were stronger predictors of either type of density. Instead, a combination of climate and edaphic variables were important, and a different set of variables was important for each measure of density. The fact that there was so little consistency between the two measures of density is additional

evidence that competition is size-symmetric in these populations (Schwinning and Weiner 1998, Weiner et al. 2001, Stoll et al. 2002); if competition were size-asymmetric and self-thinning was an important process, we would have expected to see more similar correlation magnitudes, with opposite direction, for density and biomass density.

The site variables that were mostly strongly correlated with density when all species were considered were somewhat consistent with the variables that were most strongly correlated with density for *M. laciniata* and *E. lanatum* analyzed alone. This leads us to believe that these variables are important across species in Pacific Northwest prairie communities. In particular, total inorganic nitrogen, nitrate, and minimum temperature (all season) were important for each individual analysis and the all-species analysis. However, the magnitude of the relationship of each of these variables with density was similar, reflecting the complicated ways in which climate change and resource availability interact in Pacific Northwest prairies (Pfeifer-Meister and Bridgham 2007, Pfeifer-Meister et al. 2008, 2013). Furthermore, resource availability, climate, and biotic processes all interact in complicated ways and it is difficult to disentangle their effects. Although dewpoint temperature was strongly correlated with density when all 16 populations were included, the relationship was no longer significant when the three outlier populations were removed, suggesting that this result was being driven by the outlier populations and it is not an important variable across sites. This implies that the response of prairie plants in the Pacific Northwest is both site and species idiosyncratic.

The positive relationship of density with both total inorganic nitrogen and nitrate is not surprising; as we expected, when more nutrients are available, there are more plants. Sites with lower minimum temperatures tend to have denser populations, though

this is not associated with the relationship of biomass and temperature as we expected; instead, minimum temperature seems to act independently on biomass and density. It is worth noting that temperature is closely linked with soil moisture (Huang et al. 1996), which we did not measure as part of our study. Without a direct of measure of soil moisture, we cannot say if plant density was truly responding to differences in minimum temperature alone due to a physiological temperature constraint, to differences in soil moisture as a consequence of differences in temperature, or some combination of the two. Understanding the effect of soil moisture should be an important element of future study of Pacific Northwest prairie populations.

Although the relationship showing that populations having more plants occurred at higher elevations was significant, it seems unlikely that this can be attributed to physiological properties of these species. Instead, this particular relationship could be due to the fact that higher elevation prairies could experience less human disturbance, as they may be less likely to have experienced pasture management, intensive grazing, conversion to agriculture, or urban development due to their steep slopes and relative inaccessibility. The higher populations may simply be the least disturbed by human activities.

In contrast to density, there was little consistency in the magnitude and direction of the correlations between site variables and biomass density across the individual species as well as at the all-species level. In particular, the direction of the correlation of several site variables (e.g., silt fraction) with biomass density was opposite for *M. laciniata* and *E. lanatum*. Biomass density responded much more idiosyncratically than density did to both edaphic and climate variables. However, there were a few strong

correlations when all populations were considered, suggesting that there are a few factors that are useful for understanding how biomass density varies across Pacific Northwest prairie communities. Initially, it appeared that minimum temperatures in all three seasons were the most important site variables for biomass density at the all-species level. However, the strength and direction of the correlation of several site variables with biomass density changed substantially—including a major reduction in the strength of the correlations among minimum winter and spring temperature and biomass density, as well as reversing the direction of the correlation with minimum summer temperature—when the three outlier populations were removed from the analysis, again suggesting that these populations were driving this result. Because of this, it seems likely that response of biomass density to minimum temperature is both site and species idiosyncratic. However, two edaphic variables—carbon to nitrogen ratio and soil pH—were more strongly correlated with biomass density for the remaining 13 populations. Carbon to nitrogen ratio alone explains nearly half of the variation in biomass density; it is likely that this is an important factor influencing biomass density across the region. Winter and spring precipitation was also strongly correlated with biomass density when only the non-outlier populations were considered, with a magnitude similar to the correlation with soil pH.

The fact that biomass, density, and biomass density all respond very differently to climate and edaphic variables is surprising. Biomass and density have been shown to be closely related in many systems (e.g., Weiner et al. 2001, Stoll et al. 2002), and biomass density is essentially a combination of biomass and density. This highlights the complex nature of the mechanisms governing density in Pacific Northwest prairies and how

difficult it is to separate the effects of edaphic and climate variables across species. While larger plants did produce more flowers/fruits in all species, and the correlations among each site variable and both reproduction and biomass were typically in the same direction, in most cases the magnitude of one or both of these correlations was so weak that we cannot make any definitive conclusions regarding how reproduction and biomass respond similarly or differently to site level factors. However, asexual reproduction (i.e., clonal growth) is important in many perennial plants (Schmid et al. 1995), and we observed that all of these species appear to be capable of clonal growth. Yet, we measured only sexual reproduction. Asexual growth is thought to be very similar to growth of other parts of the plant (Schmid et al. 1995), and if we had accounted for asexual reproduction, we may have observed stronger relationships between site variables and reproduction and would have been able to make a stronger conclusion regarding how biomass and reproduction are similarly affected by site variables.

Specifically concerning our hypotheses about the direction and magnitude of the relationship between precipitation and temperature variables and biomass, density, and reproduction, the results were not entirely as we expected. Temperature was only correlated with one of these measures—density—and the direction was what we expected to find: density was highest at the coolest sites. However, we expected that density would be lower at cooler sites as a consequence of higher biomass, and this was not the case; biomass and density seemed to respond independently. As discussed earlier, this indicates that competition is likely size-symmetric self-thinning is not an important process in these populations. Although we did not expect this result, the hypothesis that many Pacific Northwest prairie plant species will not be as successful under climate

temperatures is supported by our results (Pfeifer-Meister et al. 2013). If temperatures increase and density decreases without an accompanying increase in biomass, many populations could ultimately disappear. Furthermore, only minimum temperature was correlated was density, and summer—the season with the greatest moisture limitations—was most strongly correlated, which could be another indication of the importance of the interaction of temperature and soil moisture.

As previously discussed, reproduction and biomass were not correlated with temperature. Although it is not what we hypothesized, it is not surprising that reproduction was not strongly correlated with long term temperature averages for any species. Previous research has shown that flowering is typically more sensitive to short term fluctuations in temperature and the temperatures experienced in the previous growing season (Fitter et al. 1995, Marchin et al. 2015), and we did not have any short term measures of temperature. Tracking of the actual temperatures experienced by each population is in progress, and it will be useful to relate that data with reproduction data in future years. Furthermore, as the climate data we used in this study is extracted from climate models with a resolution of 800 meters, this data does not account for any microclimates that may be influencing individual populations.

In contrast, there was no support for our hypothesis regarding the relationships between precipitation and reproduction, biomass, and density; this was true at the individual species level as well as when all species were considered. This is surprising given that Pfeifer-Meister et al. (2013) found that biomass was increased with additional precipitation. However, in that study they tracked the effects of supplemental precipitation for several years. Our measure of biomass only reflects one year's growth

and may be more subject to interannual variation in precipitation. There is no guarantee that the relative amount of precipitation received at each site in the growing season prior to our survey corresponded to the long term precipitation averages. The 2014-2015 growing season was abnormally dry, particularly in Washington, ("Climatological Rankings" 2016) and it is difficult to assess how this could have affected our results with only a single year of data. Biomass density, on the other hand, was strongly correlated with winter and spring precipitation; the populations with the most biomass per square meter were at sites that receive the most precipitation. We expected this result, but again we expected it to be due to greater biomass at sites with more precipitation, which was not the case. It is very surprising that the correlations between each site variable and biomass, density, and biomass density were so different.

This comparison of manipulative experiment and observational study data could suggest that the underlying mechanism responsible for increased biomass under artificial heating does not fully explain differences in biomass in natural populations; in the more variable natural environment (e.g., different pedogenic processes for each population), it is not possible to attribute our observations to any single mechanism. It is also possible that the differences in the results of the natural and experimental populations could be due to a threshold response, particularly in regard to temperature. The difference in temperature experienced by each population of a single species was often less than 2.5°C (the amount of warming in Pfeifer-Meister et al. 2013)—perhaps due to the physiological tolerances of each species—and it is possible that we would have found stronger correlations if we had been able to locate populations with larger differences in temperature.

Pacific Northwest prairies have become a rare ecosystem; land-use change is one of the major culprits (Bachelet et al. 2011). Land use conversion is not a random process, and many prairies are found on soils that are considered very desirable for agriculture (e.g., Mollisols; Liu et al. 2012). The extant populations studied here are not necessarily the populations that were historically the most successful; it is possible that the remaining populations are at marginal sites and do not represent ideal conditions. Yet it is also possible that some species naturally favor the sites that were least likely to be converted to agriculture. Unfortunately, it is nearly impossible to determine which of these may be the case for each species, as there are very few natural prairies left to select from. Although our anecdotal field observations combined with analysis of variance suggested that some species, such as *E. lanatum,* favors sites with deeper soils and fewer rocks that are more suitable for farmland, this was not found to be true when the specific correlations were assessed.

Based on the results of this analysis, it seems that individual species response to edaphic and climate variables is idiosyncratic for biomass and reproduction. Although Pfeifer-Meister et al. (2013) found generally consistent responses to artificial warming among species within a range group, other studies (e.g., Zavaleta et al. 2003) have found that it is very difficult to predict species response to temperature and precipitation. While our results are more in line with the findings of Zavaleta et al. (2003), neither do they entirely contradict Pfeifer-Meister et al. (2013), as we only had one species per range group and all of our populations are within current range limits. Our findings are consistent with a number of other studies considering both biotic and abiotic factors in a variety of systems (Parmesan and Yohe 2003, Lloret et al. 2004, Penuelas et al. 2007,

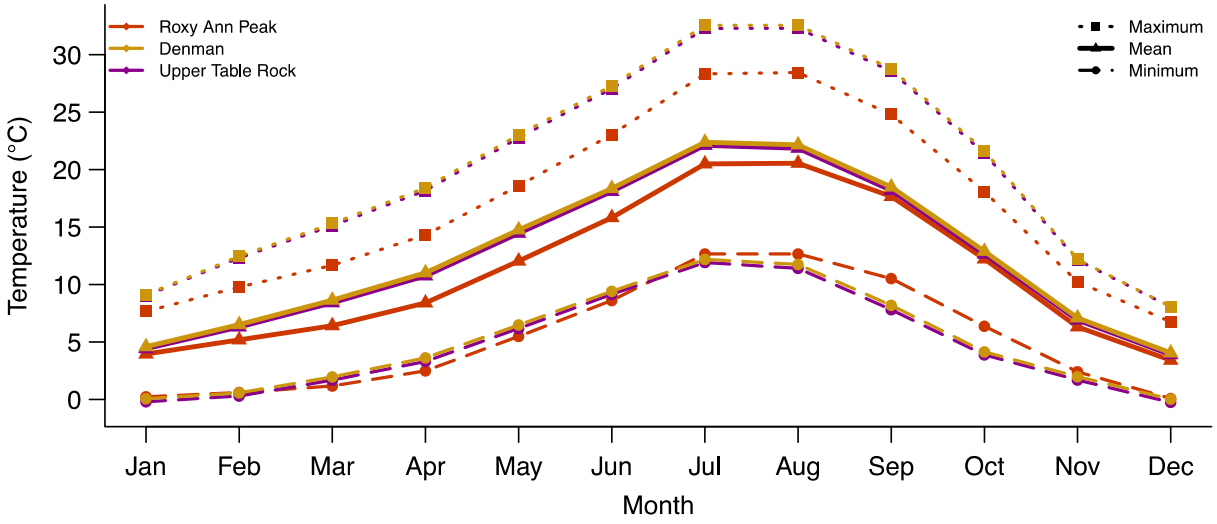
Doak and Morris 2010, Corlett and Westcott 2013, Rumpf et al. 2014). Furthermore, there was no clear dominance of edaphic or climate variables across sites, and no particular variables that had a stronger correlation with biomass or reproduction for any species. Although the ordination clearly differentiated the three regions, neither axis was composed primarily of either climate or edaphic variables, and the linear model relating standardized biomass and the axes explained very little of the variation in biomass. Instead, it seems likely that it is a complex interaction of both edaphic and climate variables, as well as other factors such as competition and disturbance, that determines where populations are found and how they are structured. Density seems to be a better indicator of how site variables affect demographic processes in plant communities when compared to measurements of biomass and reproduction for a single year, though it also is affected by both edaphic and climate variables. This also highlights the importance of collecting multi-year data sets, as suggested by many authors (e.g., Doak and Morris 2010). Additionally, because we only collected data on a single species at each population and effectively ignored all other plants present, it is difficult to make definitive conclusions regarding inter- and intraspecific competition at each site. Future work at these populations will involve collection of normalized difference vegetation index (NDVI) data, which is a measure of total above ground primary productivity and can be used as an indicator of competition (Huemmrich et al. 1999, Verhulst et al. 2009).

CHAPTER III

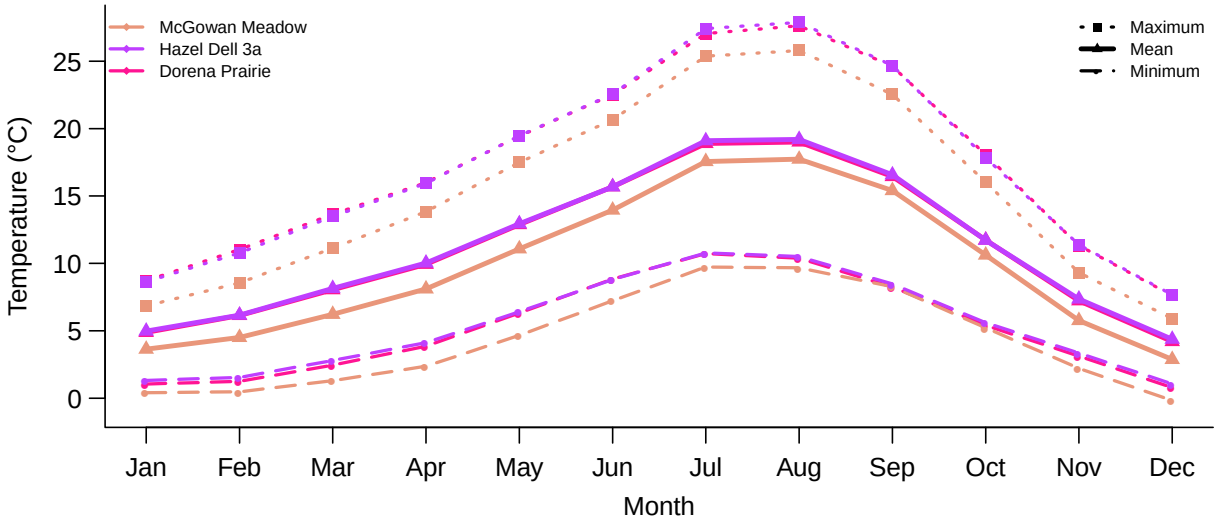
CONCLUSIONS

In this observational study, we found that biomass and reproduction in four species native to Pacific Northwest prairies were not strongly correlated with any of the site variables that we analyzed, and the direction of each correlation depended on the individual species. Our finding that species response is idiosyncratic is not entirely unexpected given similar findings in many studies of other systems (Morris and Doak 2002, Parmesan and Yohe 2003, Lloret et al. 2004, Jump and Peñuelas 2005, Corlett and Westcott 2013, Rumpf et al. 2014). We also found that competition appears to be size-symmetric in these populations, which was surprising. However, because we did not assess the overall competitive environment that these individual populations exist in, nor did we quantitatively assess other biotic factors, more study is needed on how density and spatial patterning acts in Pacific Northwest prairies.

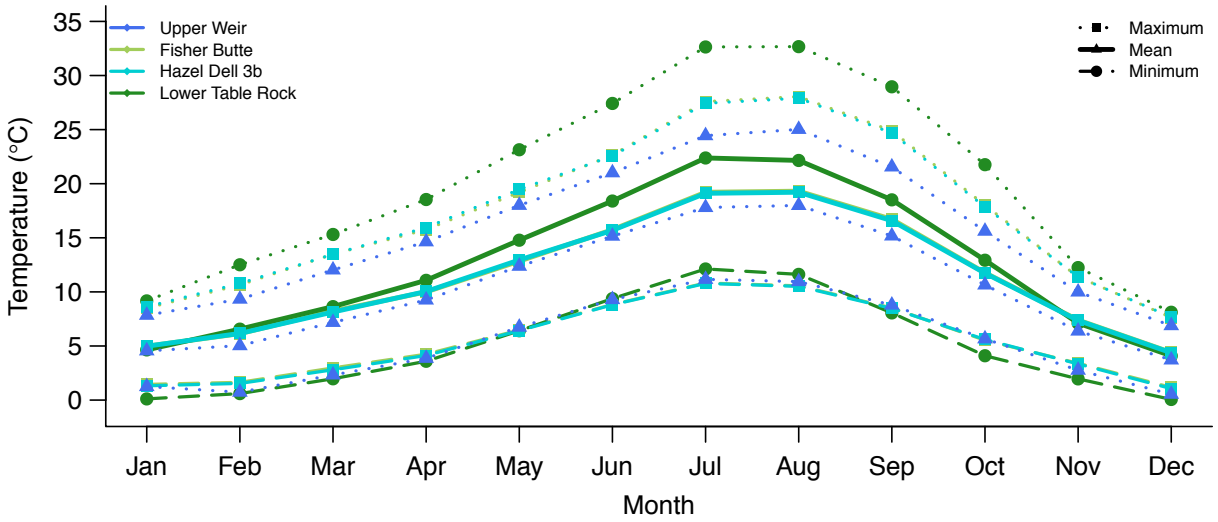
Comparing natural populations with experimental populations highlights the difficulties related to making specific predictions about the future when underlying mechanisms are still poorly understood. As the response of individual species has been shown to be strongly variable, it is difficult to make broad conclusions that will apply for every species in a community. Management decisions regarding individual species must be carefully assessed and based on multiple lines of evidence, rather than overall blanket statements about the future of prairies in the Pacific Northwest.



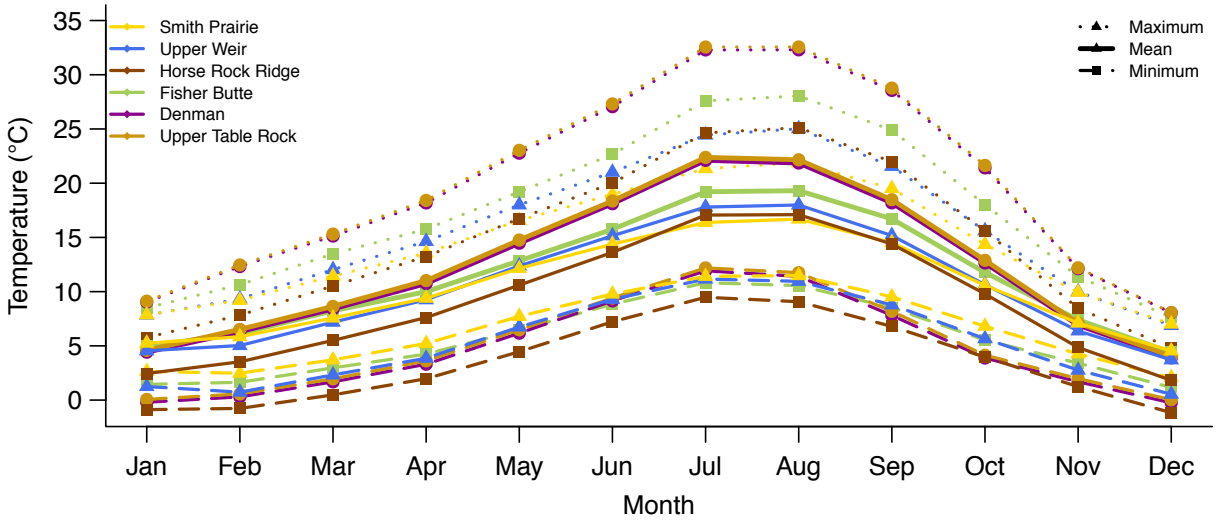
Supplemental Figure 1. Maximum, mean, and minimum temperatures throughout the year for *R. austro-oreganus* sites based on 1980-2010 climate normals.



Supplemental Figure 2. Maximum, mean, and minimum temperatures throughout the year for *S. malviflora* ssp. *virgata* sites based on 1980-2010 climate normals.



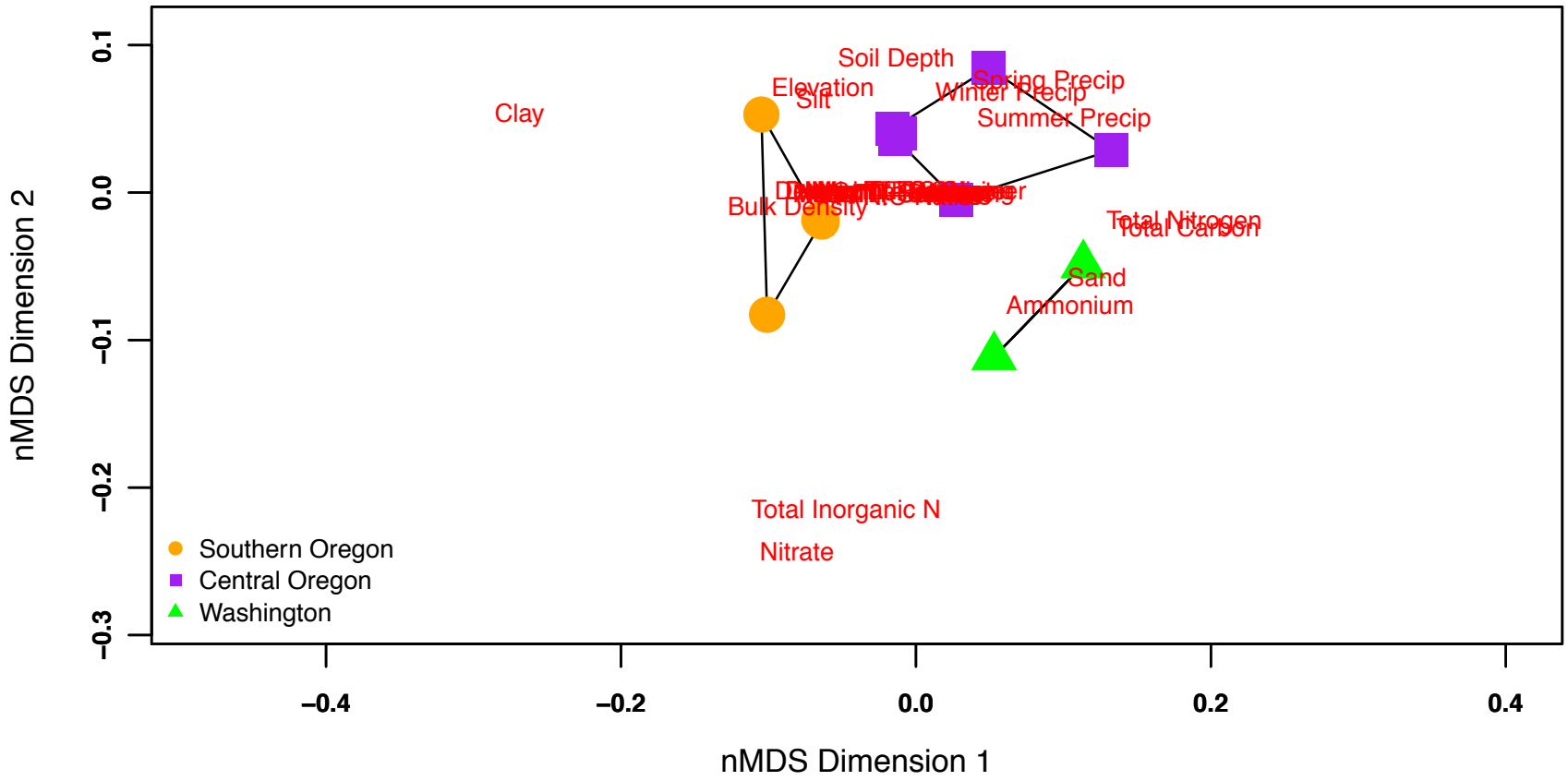
Supplemental Figure 3. Maximum, mean, and minimum temperatures throughout the year for *M. laciniata* sites based on 1980-2010 climate normals.



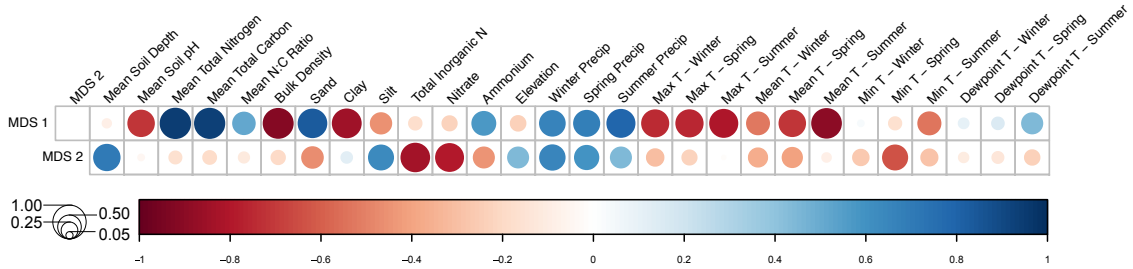
Supplemental Figure 4. Maximum, mean, and minimum temperatures throughout the year for *E. lanatum* sites based on 1980-2010 climate normals.

Supplemental Table 1. Date of census for all populations.

Species	Range Group	Site	Region	Census Date	Reprod-uction Update Date
E. lanatum	W	Upper Weir Prairie	WAS	6/12/15	N/A
		Smith Prairie	WAS	6/20/15	N/A
		Fisher Butte	COR	6/17/15	N/A
		Horse Rock Ridge	COR	6/15/16 & 6/16/15	N/A
		Denman Wildlife Area	SOR	5/22/15	N/A
		Upper Table Rock	SOR	5/21/15 & 5/22/15	N/A
Microseris laciniata	HNL	Upper Weir Prairie	WAS	6/13/15	N/A
		Fisher Butte	COR	6/17/15	N/A
		Hazel Dell 3b	COR	6/9/15	N/A
		Lower Table Rock	SOR	5/22/15	N/A
S. malviflora ssp. *virgata*	INL	Dorena Prairie	COR	5/18/15	N/A
		Hazel Dell 3a	COR	5/18/15 & 5/19/15	N/A
		McGowan Meadow	COR	6/25/15	N/A
Ranunculus austro-oreganus	LNL	Denman Wildlife Area	SOR	3/20/15	N/A
		Roxy Ann Peak	SOR	3/21/15	4/19/15
		Upper Table Rock	SOR	3/20/15	4/18/15



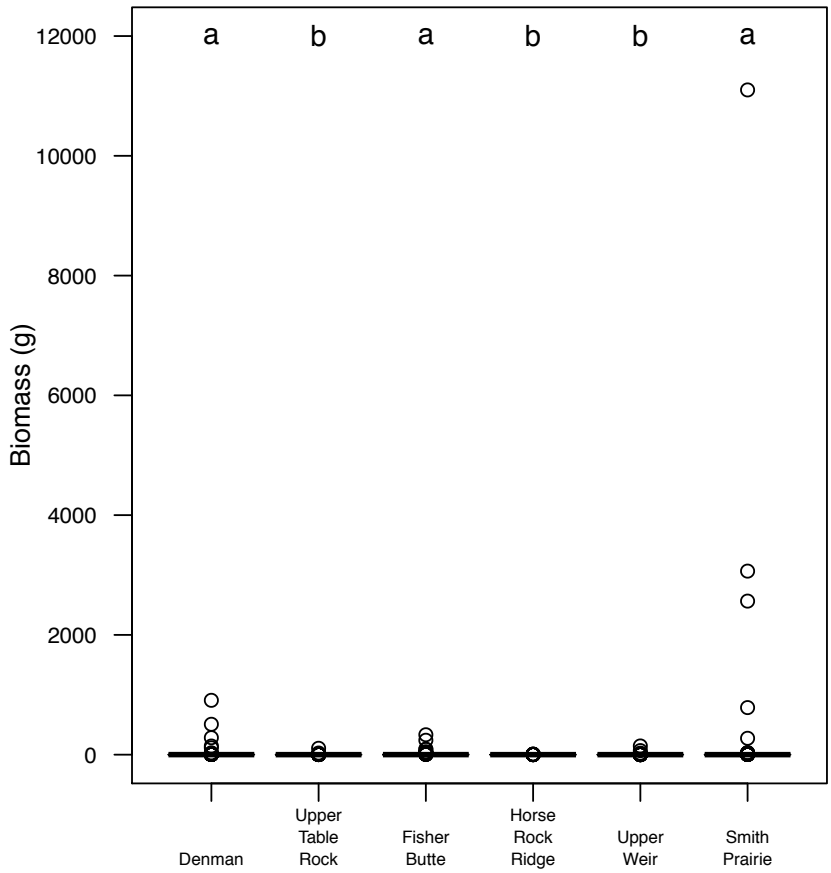
Supplemental Figure 5. NMDS and site variable scores.



Supplemental Figure 6. Correlations between each of the edaphic and climate variables and the NMDS axes.

Supplemental Table 2. NMDS axis scores by variable ("species").

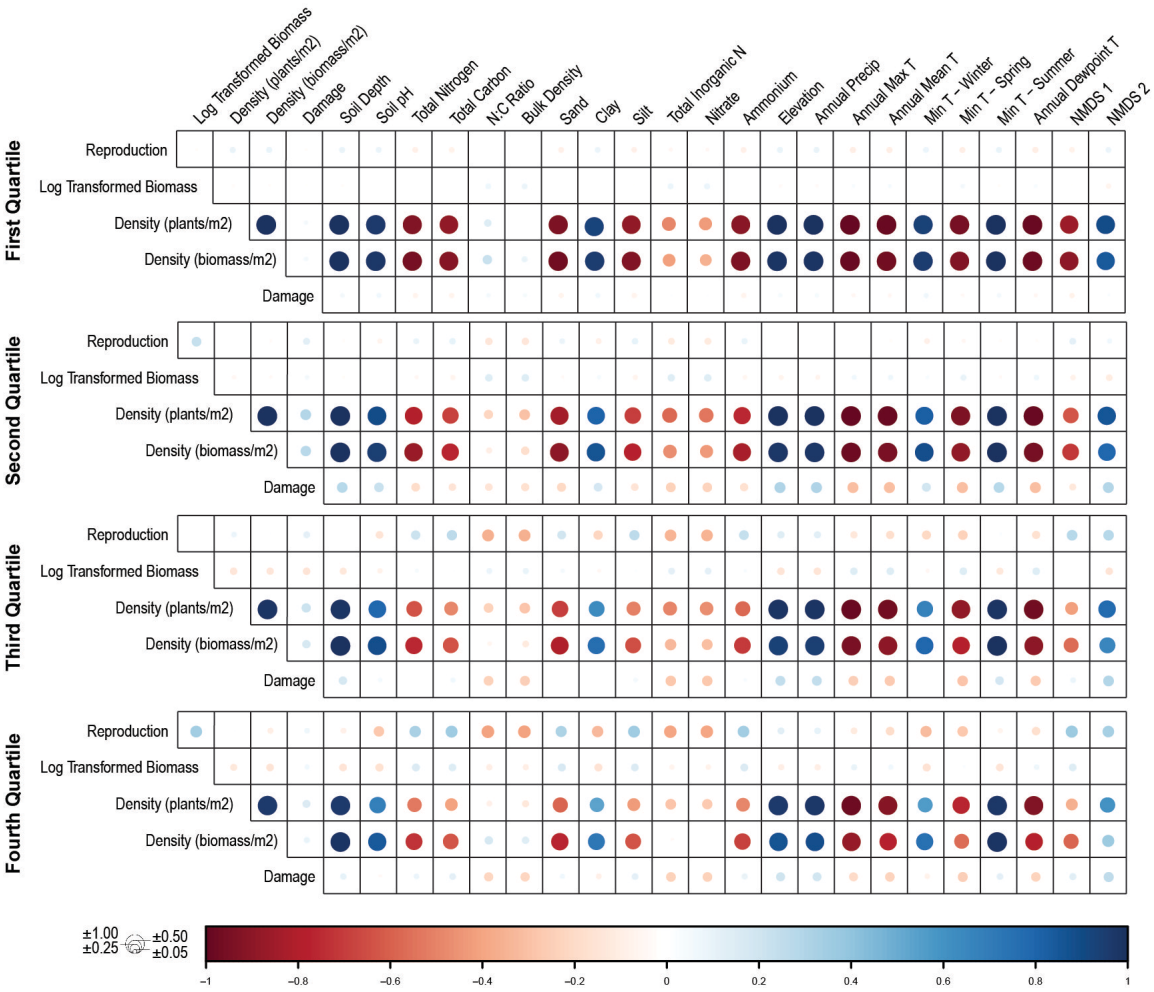
	NMDS Axis 1	NMDS Axis 2
Clay	-0.26877	0.05237
Nitrate	-0.08065	-0.24319
Bulk Density	-0.08000	-0.01118
Silt	-0.06955	0.06328
Elevation	-0.06313	0.07131
Total Inorganic N	-0.04733	-0.21611
Soil pH	-0.02862	-0.00087
Soil Depth	-0.01333	0.09026
Max Temperature - Summer	-0.01311	-0.00010
Max Temperature - Spring	-0.01241	-0.00042
Mean Temperature - Summer	-0.01225	-0.00016
Max Temperature - Winter	-0.01176	-0.00033
Mean Temperature - Spring	-0.01176	-0.00044
Mean Temperature - Winter	-0.01134	-0.00028
Min Temperature - Summer	-0.01134	-0.00023
Min Temperature - Spring	-0.01108	-0.00047
Min Temperature - Winter	-0.01091	-0.00024
Dewpoint Temperature - Winter	-0.01083	-0.00015
Dewpoint Temperature - Spring	-0.01080	-0.00017
Dewpoint Temperature - Summer	-0.01043	-0.00028
N:C Ratio	0.00156	-0.00252
Winter Precipitation	0.06460	0.06701
Spring Precipitation	0.09021	0.07489
Summer Precipitation	0.10050	0.04932
Ammonium	0.10453	-0.07604
Sand	0.12294	-0.05699
Total Nitrogen	0.18191	-0.02032
Total Carbon	0.18443	-0.02342



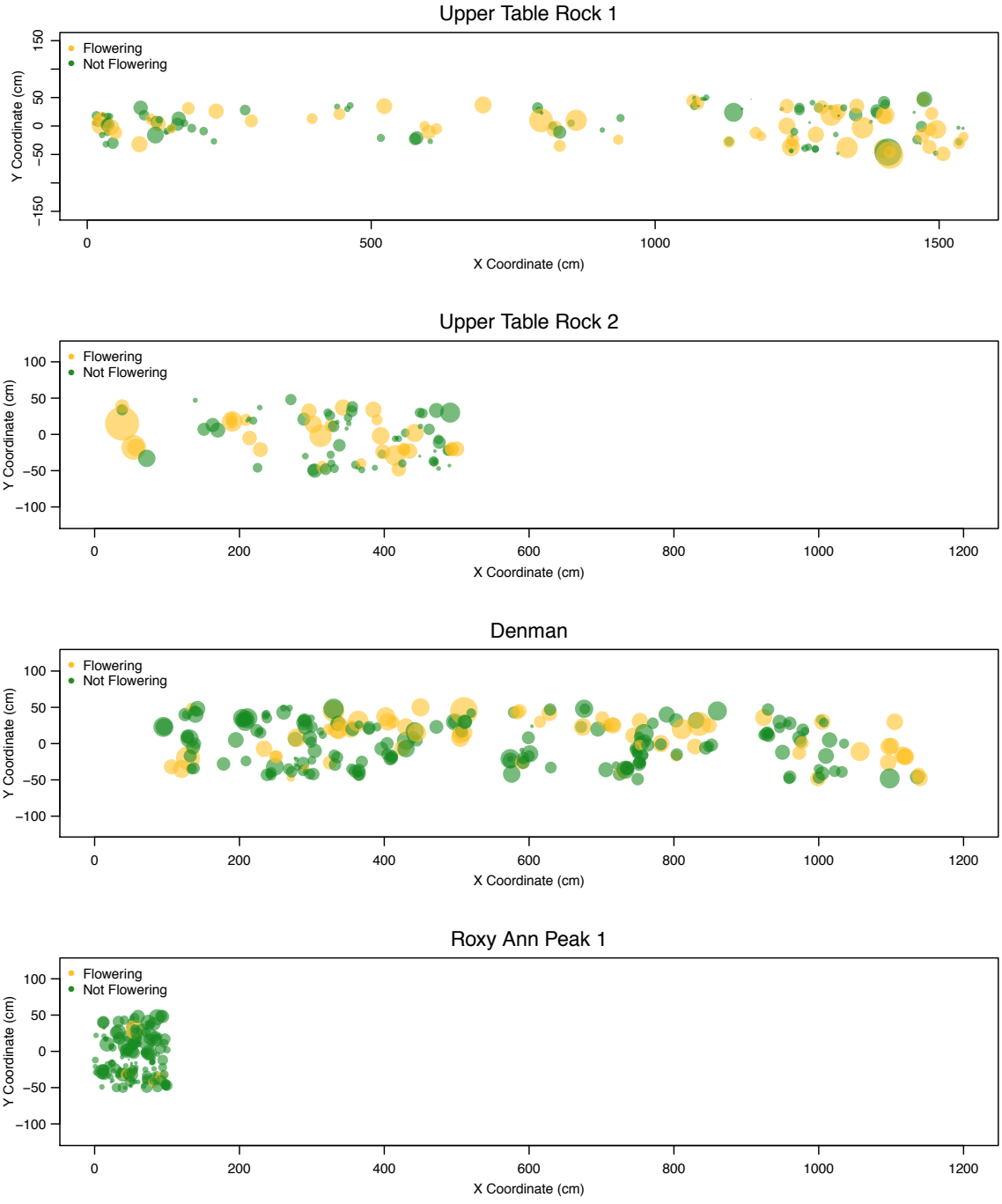
Supplemental Figure 7. Boxplot of biomass (all plants) for the six *E. lanatum* populations. Different letters indicate significant differences among sites ($p < 0.05$).

	Log Transformed Biomass	Density (plants/m2)	Density (biomass/m2)	Damage	Soil Depth	Soil pH	Total Nitrogen	Total Carbon	N:C Ratio	Bulk Density	Sand	Clay	Silt	Total Inorganic N	Nitrate	Ammonium	Elevation	Annual Precip	Annual Max T	Annual Mean T	Min T – Winter	Min T – Spring	Min T – Summer	Annual Dewpoint T	NMDS 1	NMDS 2
Reproduction	46	−12	−14	12	−14	−18	19	19	−12	−11	18	−19	19	−6	−7	19	−10	−10	10	8	−18	5	−14	9	19	−2
Log Transformed Biomass		−29	−24	16	−25	−12	4	−3	33	34	6	−4	−3	39	38	1	−33	−32	32	35	−6	38	−26	35	−7	−40
Density (plants/m2)			99	12	99	87	−75	−62	−19	−26	−79	75	−64	−51	−48	−70	99	99	−99	−97	78	−91	99	−98	−56	82
Density (biomass/m2)				11	100	93	−83	−73	−4	−11	−87	83	−74	−38	−35	−79	96	96	−96	−92	86	−84	100	−93	−67	72
Damage					11	7	−4	−2	−9	−10	−5	4	−2	−13	−12	−3	13	13	−13	−14	5	−14	11	−14	−1	14

Supplemental Figure 8. Raw correlations, multiplied by 100, for each variable for *R. austro-oreganus.*



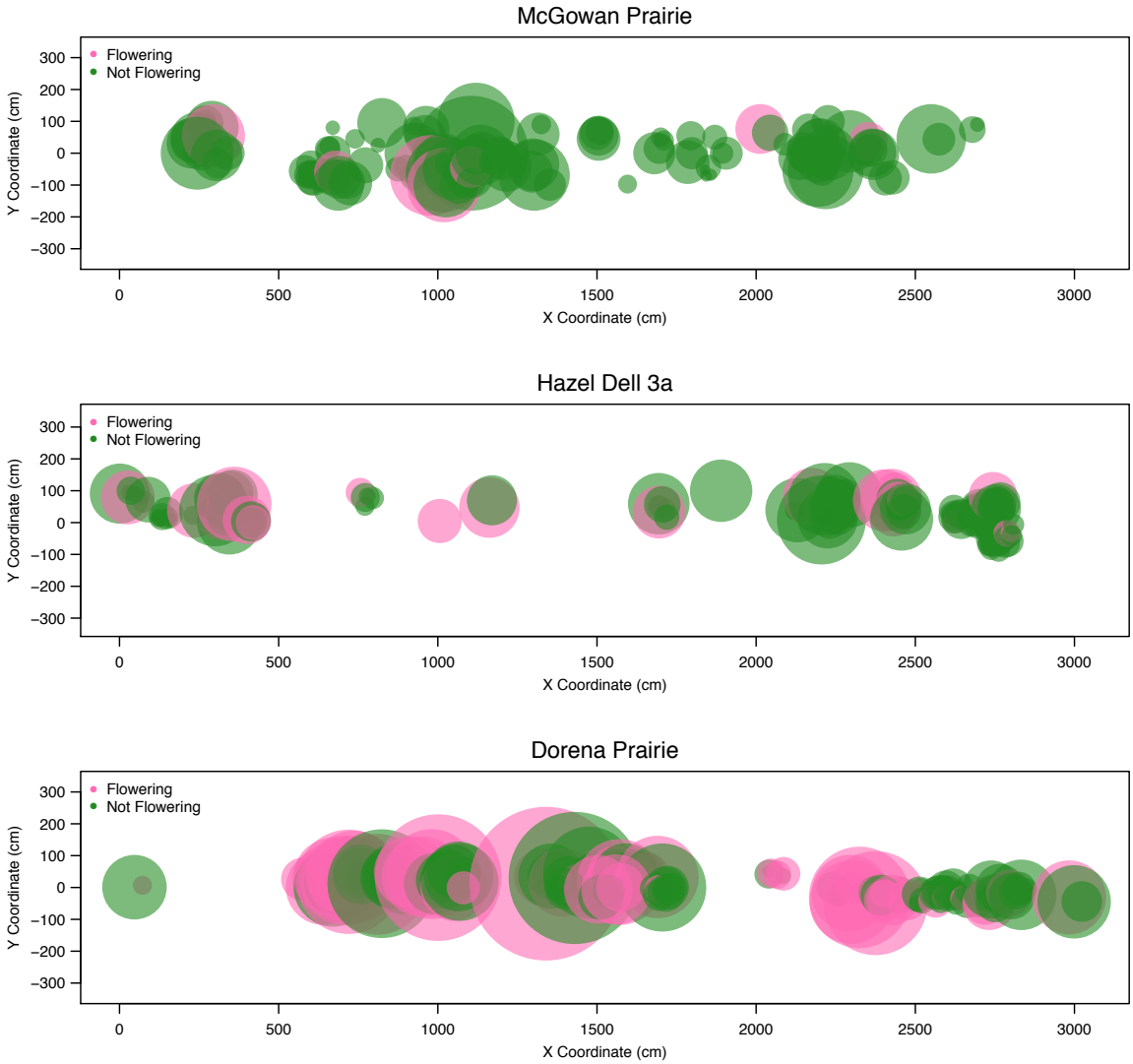
Supplemental Figure 9. Table of correlations for plant, edaphic, and climate variables for the *R. austro-oreganus* plants, divided into quartiles by biomass.



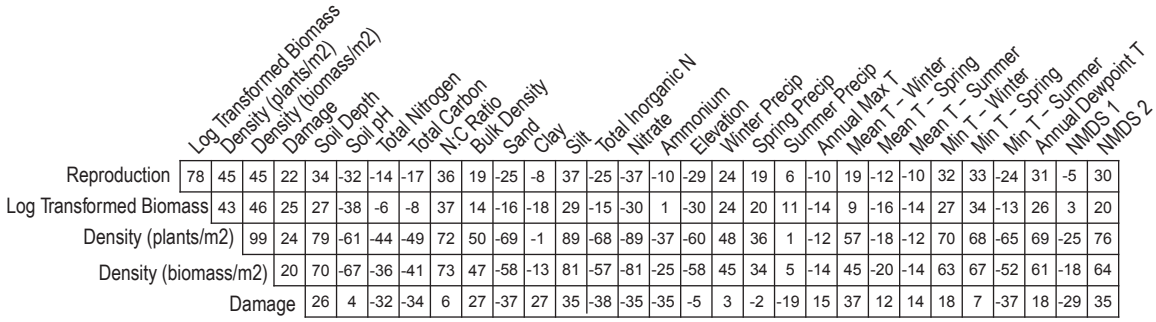
Supplemental Figure 10. Map of location and relative size for each plant at each *R. austro-oreganus* transect. Plants colored in yellow were flowering or had fruit at the time of census; plants colored in green did not exhibit sexual reproduction in the year of the census.

	Log Transformed Biomass	Density (plants/m2)	Density (biomass/m2)	Damage	Soil Depth	Soil pH	Total Nitrogen	Total Carbon	N:C Ratio	Bulk Density	Sand	Clay	Silt	Total Inorganic N	Nitrate	Ammonium	Elevation	Annual Precip	Annual Max T	Annual Mean T	Annual Min T	Annual Dewpoint T	NMDS 1	NMDS 2
Reproduction	43	10	17	12	−18	17	6	6	−7	−3	17	5	−14	2	−14	17	−3	−4	6	4	2	1	8	−14
Log Transformed Biomass		4	23	24	−25	21	24	23	−24	−19	22	−6	−14	−10	−32	21	10	6	−4	−7	−10	−13	26	−13
Density (plants/m2)			78	15	−72	82	−61	−63	58	75	82	96	−95	91	14	83	−92	−95	97	95	91	87	−53	−95
Density (biomass/m2)				7	−100	100	2	0	−6	16	100	56	−94	45	−52	100	−46	−55	60	54	44	36	12	−93
Damage					−6	8	−14	−14	14	15	8	16	−12	16	9	8	−16	−16	16	16	16	16	−13	−12

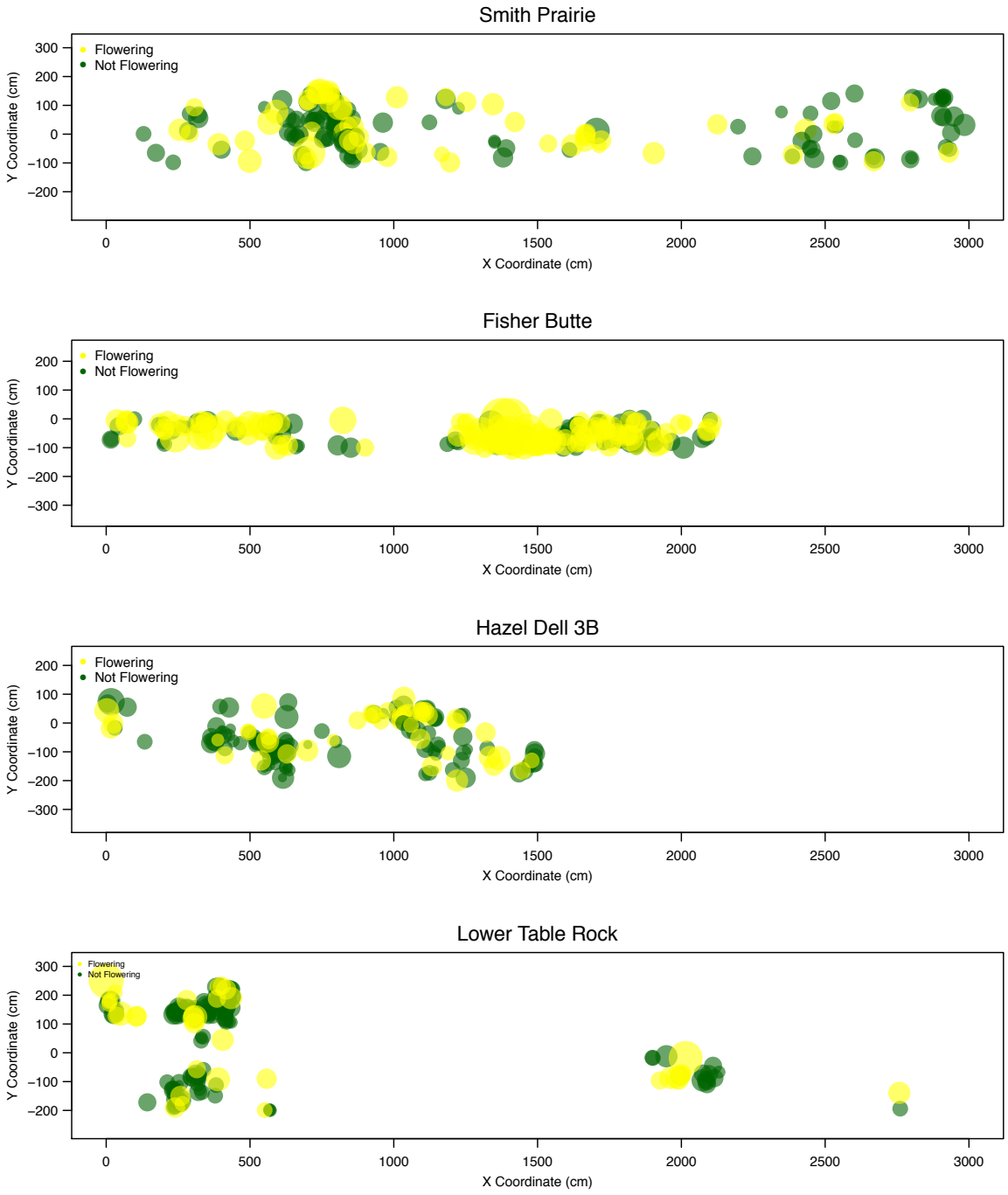
Supplemental Figure 11. Raw correlations, multiplied by 100, for each variable for *S. malviflora* ssp. *virgata.*



Supplemental Figure 12. Map of location and relative size for each plant at each *S. malviflora* ssp. *virgata* transect. Plants colored in pink were flowering or had fruit at the time of census; plants colored in green did not exhibit sexual reproduction in the year of the census.



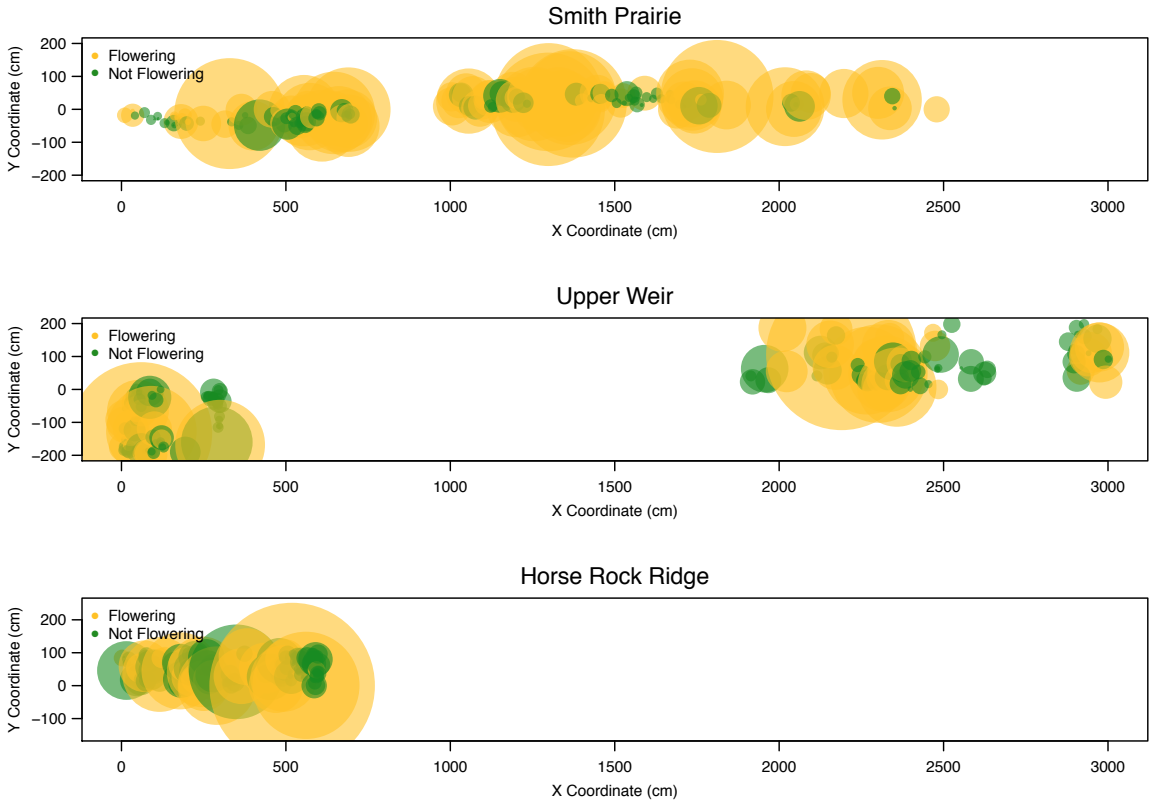
Supplemental Figure 13. Raw correlations, multiplied by 100, for each variable for *M. laciniata.*



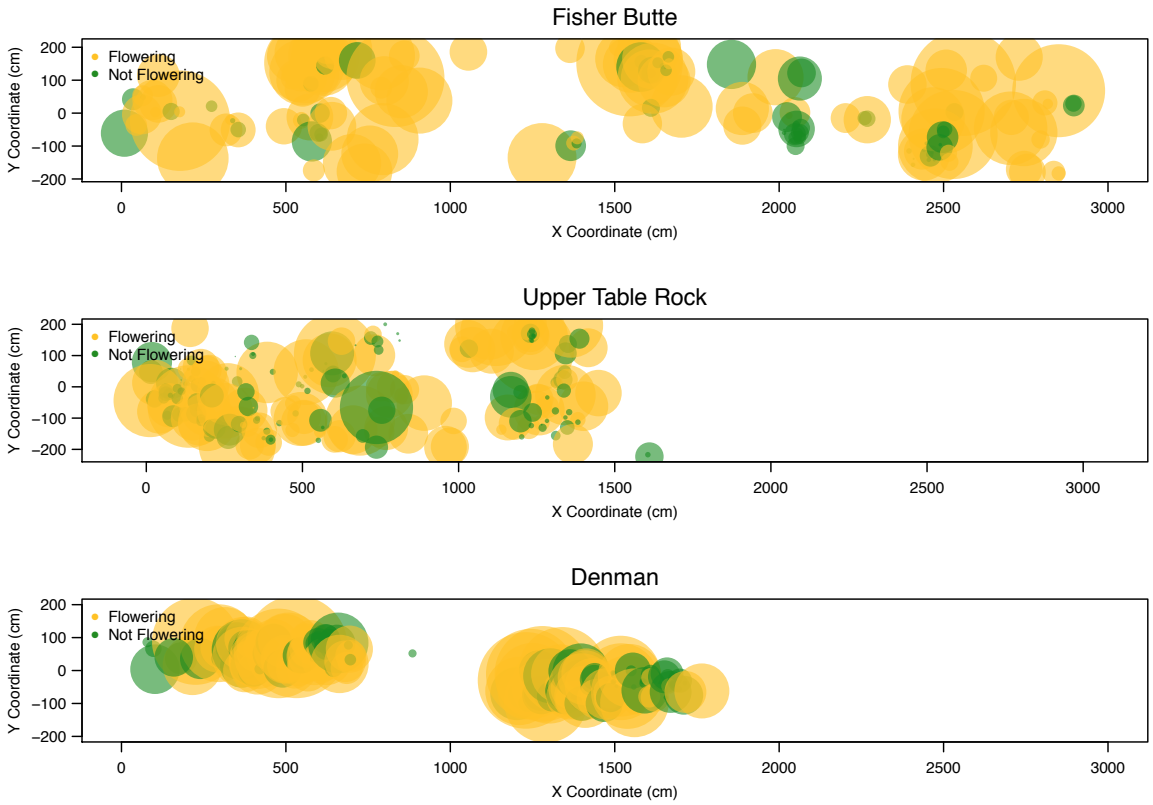
Supplemental Figure 14. Map of location and relative size for each plant at each *M. laciniata* transect. Plants colored in yellow were flowering or had fruit at the time of census; plants colored in green did not exhibit sexual reproduction in the year of the census.

	Log Transformed Biomass	Density (plants/m2)	Density (biomass/m2)	Damage	Soil Depth	Soil pH	Total Nitrogen	Total Carbon	N:C Ratio	Bulk Density	Sand	Clay	Silt	Total Inorganic N	Nitrate	Ammonium	Elevation	Winter Precip	Spring Precip	Summer Precip	Annual Max T	Mean T – Winter	Mean T – Spring	Mean T – Summer	Min T – Winter	Min T – Spring	Min T – Summer	Annual Dewpoint T	NMDS 1	NMDS 2
Reproduction	63	4	3	25	-7	15	-11	-10	-8	12	-10	18	1	14	15	-8	6	-11	-14	-14	13	8	16	14	-6	1	5	-7	-15	-9
Log Transformed Biomass	8	0	37	14	-4	-7	-8	15	11	-8	9	5	9	10	-15	-5	3	1	-1	1	7	1	1	6	4	2	9	-6	1
Density (plants/m2)	58	10	-31	28	19	17	19	-5	39	11	-66	76	76	-32	12	-27	1	15	-34	-24	-29	-32	14	15	20	-24	16	-66
Density (biomass/m2)	25	-8	-17	34	35	13	-9	73	-45	-74	49	47	7	-59	-56	-29	-4	-70	28	-49	-69	79	80	76	37	41	-70
Damage	-8	2	4	5	-8	0	17	-11	-17	9	9	3	-11	-20	-13	-7	-13	9	-7	-12	17	19	19	4	6	-17

Supplemental Figure 15. Raw correlations, multiplied by 100, for each variable for *E. lanatum*.



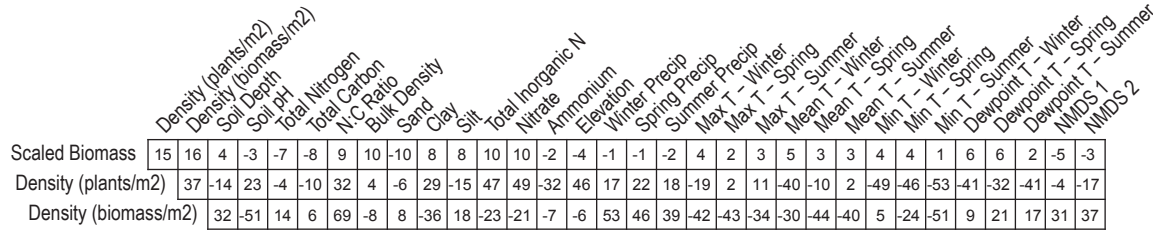
Supplemental Figure 16. Map of location and relative size for each plant at the three northern *E. lanatum* populations. Plants colored in yellow were flowering or had fruit at the time of census; plants colored in green did not exhibit sexual reproduction in the year of the census.



Supplemental Figure 17. Map of location and relative size for each plant at the three southern *E. lanatum* populations. Plants colored in yellow were flowering or had fruit at the time of census; plants colored in green did not exhibit sexual reproduction in the year of the census.

	Density (plants/m2)	Density (biomass/m2)	Soil Depth	Soil pH	Total Nitrogen	Total Carbon	N:C Ratio	Bulk Density	Sand	Clay	Silt	Total Inorganic N	Nitrate	Ammonium	Elevation	Winter Precip	Spring Precip	Summer Precip	Max T – Winter	Max T – Spring	Max T – Summer	Mean T – Winter	Mean T – Spring	Mean T – Summer	Min T – Winter	Min T – Spring	Min T – Summer	Dewpoint T – Winter	Dewpoint T – Spring	Dewpoint T – Summer	NMDS 1	NMDS 2
Scaled Biomass	-9	4	-1	-6	-2	-3	9	5	0	-4	4	8	8	2	-11	0	-1	0	3	1	0	6	3	-1	6	7	-5	11	11	9	1	-6
Density (plants/m2)	2	27	34	-21	-22	-14	16	-32	58	-9	-1	1	-35	70	-4	-3	-8	-21	-15	-2	-26	-24	9	-15	-32	56	-65	-61	-59	-30	17	
Density (biomass/m2)	-7	-16	19	20	15	0	49	-28	-49	38	36	7	-32	-35	-20	-6	-23	-40	-51	17	-21	-43	58	54	39	7	14	32	22	-50		

Supplemental Figure 18. Raw correlations, multiplied by 100, for each variable for standardized biomass and density for all populations.



Supplemental Figure 19. Raw correlations, multiplied by 100, for each variable for standardized biomass and density for the 13 populations that remain after outliers are removed.

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